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TRANSACTIONS

OF THE

ROYAL SOCIETY OF SOUTH AFRICA

VOLUME XXXVI—PART III

1961

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CAPE TOWN
PUBLISHED BY THE SOCIETY
—
1961

Issued October, 1961

Price R1.90

Q 85
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GRAVITY OBSERVATIONS AT MARION ISLAND, TRISTAN DA CUNHA AND GOUGH ISLAND

By B. L. Weid *
Geological Survey, Pretoria

(Communicated by L. E. Kent)

(Read March 15, 1961)

Stations were established with a Worden geodetic-type gravimeter on Marion Island, Tristan da Cunha and Gough Island. The gravity values at these stations, viz. two on Tristan da Cunha and one each on Marion and Gough, were determined relative to the international gravity base at Mowbray, Cape Town.

Two methods for extending the range of the gravimeter by operating it in a tilted position are described in an appendix. These methods had to be adopted for determining the gravity value at Marion.

Introduction

The Geological Survey was able to avail itself of an opportunity to establish gravity stations on Marion Island, Tristan da Cunha and Gough Island during the annual relief voyage of Meteorological personnel for which the Department of Transport had chartered the R.R.S. *Shackleton*.

In view of the increasing attention being given to geophysical investigations at sea it was felt that such preliminary gravity stations may be useful in conjunction with future gravity work in these regions.

The gravity observations were carried out with a geodetic-type Worden gravimeter (serial number 97).

The Gravity Determinations

Marion Island was visited first and after returning to Cape Town the voyage to Tristan da Cunha and Gough Island was undertaken.

The gravity determinations are discussed in the sequence of observations.

(*a*) *Marion Island.* As the gravimeter had a restricted range and could be operated only as far south as about 44° latitude, a special method of observation was adopted whereby the normal operating range of the instrument was extended. This method is described in detail in the appendix.

The gravity station was established on a square concrete slab at the base of the inner crane at Gunner's Point (see fig. 2).

(*b*) *Tristan da Cunha.* Two gravity stations were established on the island. Station No. 1 was chosen at the magnetic station B, which is directly in line with the light beacon and the flagstaff along the transit line 174°, shown on Admiralty Chart

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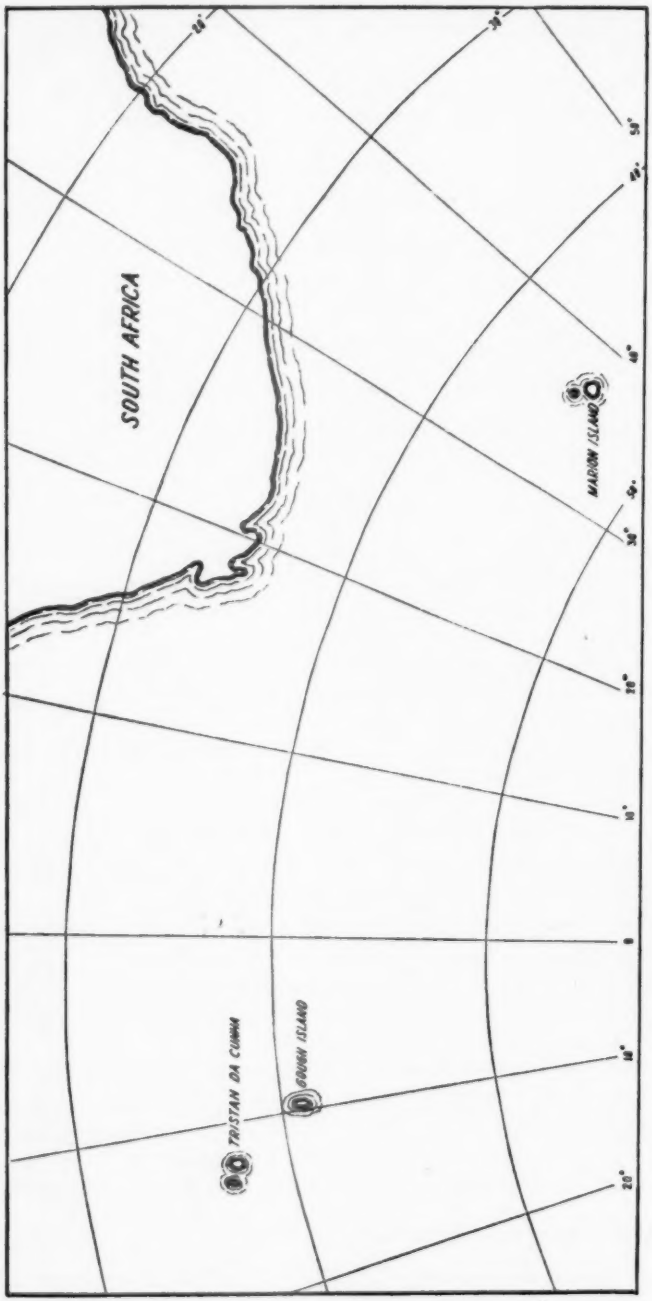


FIG. 1. Map showing the positions of Marion Island, Tristan da Cunha and Gough Island.

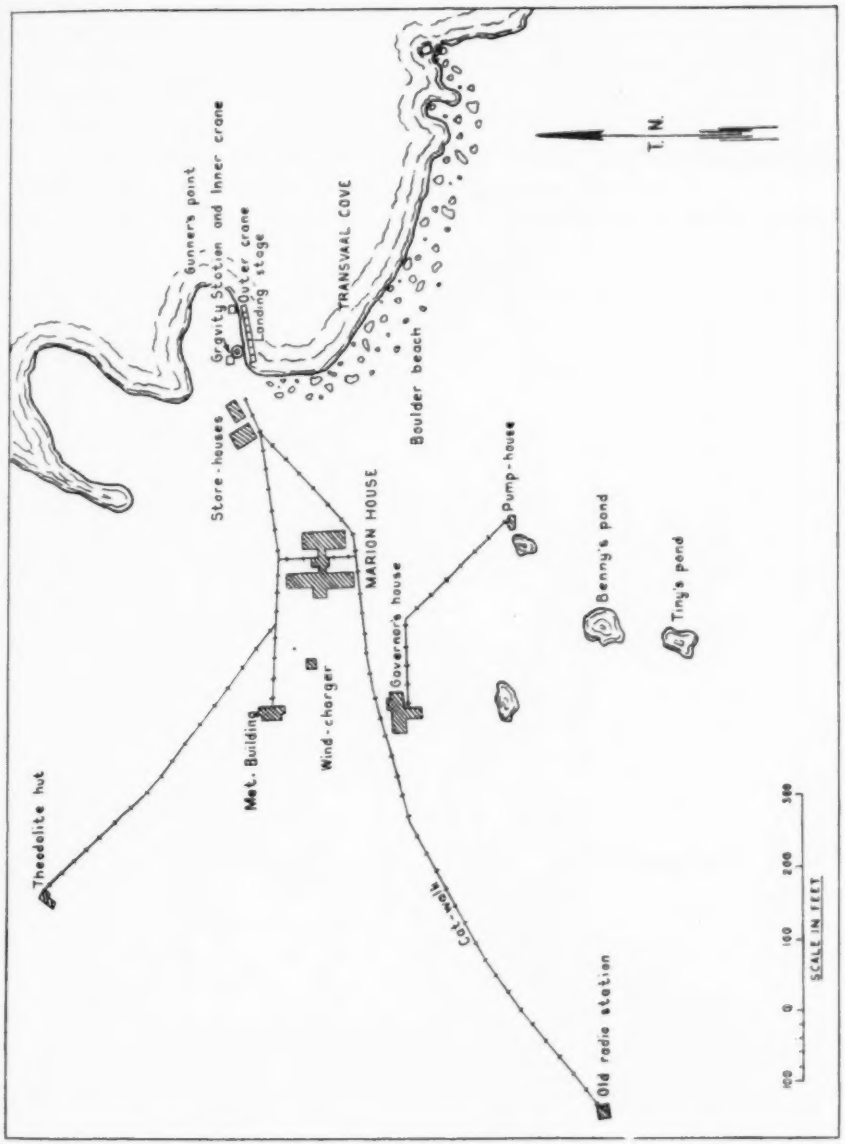


FIG. 2. Plan showing locality of the gravity station at Marion Island.

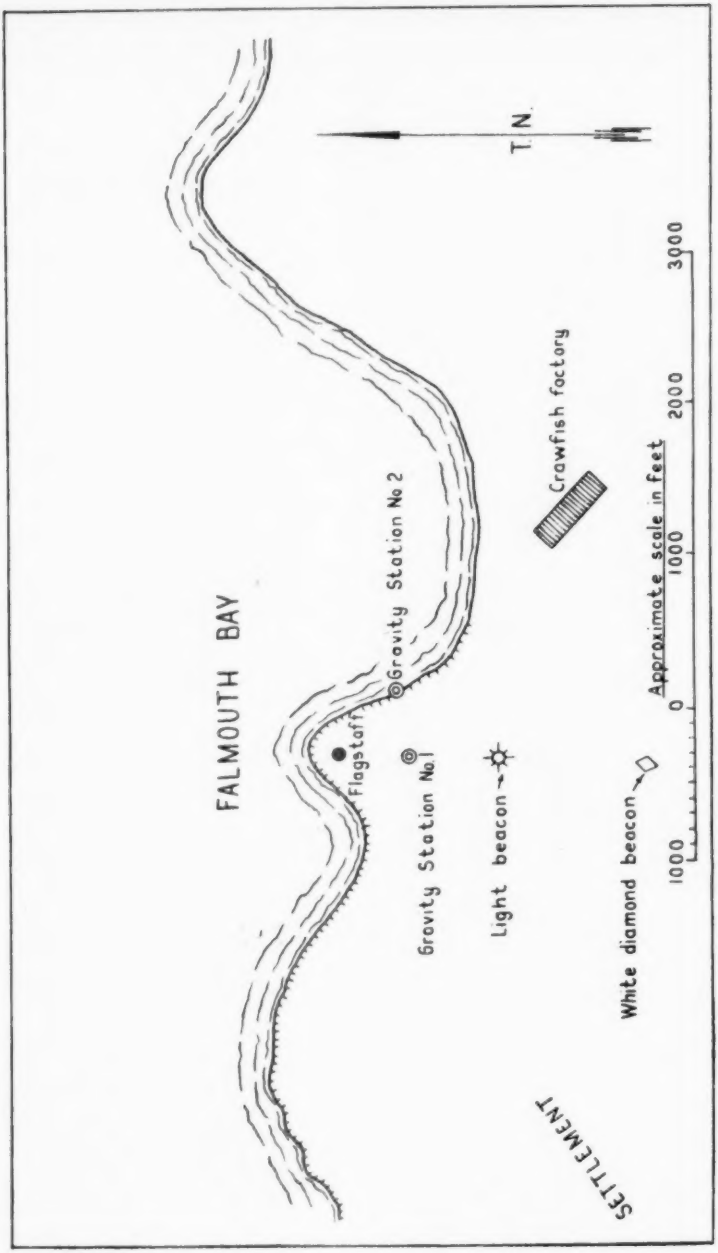


FIG. 3. Locality sketch showing the gravity stations at Tristan da Cunha.

1769. The station, which is marked by a brass bolt set in concrete, is 292 feet from the flagstaff measured in the direction of the light beacon.

Station No. 2 was established at the landing beach below the crawfish factory. The reading was taken on top of a concrete block, roughly 2 feet square and 4 feet high, situated at the foot of the cliff.

Both gravity stations are indicated in fig. 3.

(*c*) *Gough Island.* The gravity observations were made at the Meteorological Station which is practically on the beach in the mouth of the glen.

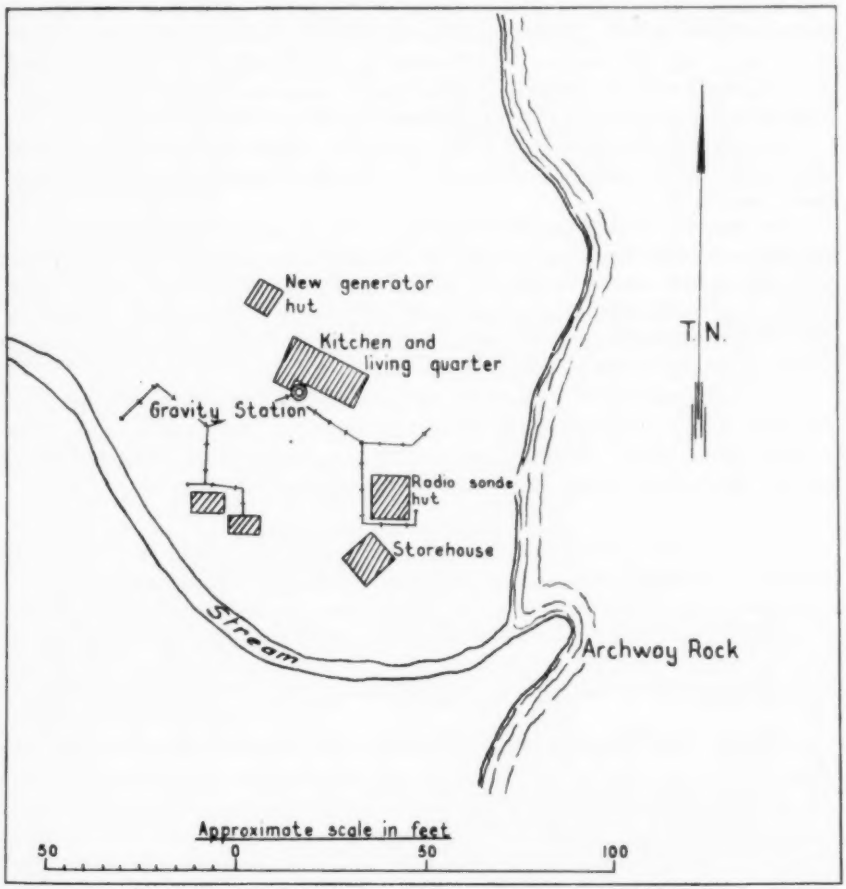


FIG. 4. Sketch showing locality of the gravity station on Gough Island.

The gravity station is on a concrete slab at the entrance to the kitchen and living quarters (see fig. 4).

The Accuracy of the Gravity Determinations

The accuracy to which the final observed gravity values could be calculated depended on how successfully the instrumental drift could be determined.

In this respect, it may be stated that the Worden gravimeter is characterized by a relatively small drift rate which, apart from minor erratic variations due to handling during operation, can be interpreted as a linear increase when measured over a period of several days.

As the drift on this survey was determined as a linear interpolation between observations at a specially established station in the Cape Town harbour, immediately before and after each voyage, errors due to erratic variations could not be eliminated. This station was later tied to the Mowbray pendulum station ($g = 979{\cdot}6468$ gal $\pm 0{\cdot}3$ milligal) so that the gravity values, which were determined on the islands, could be computed in terms of the international gravity network.

Aboard ship, the instrument in its standard container was securely supported with sponge rubber packing to protect it from engine vibration and ship movement during bad weather.

The first trip, to Marion Island and back, took 14 days. During this period the gravimeter reading drifted only a total of 1·7 milligal, i.e. roughly 0·12 milligal per day. During the second voyage, to Tristan da Cunha and Gough Island which lasted 18 days, the average drift rate increased to approximately 0·26 milligal per day. This increase in the drift can probably be ascribed to the more stormy conditions at sea. (The ship at times rolled as much as 25°.)

It is estimated that in general the effect of the drift could be eliminated to an accuracy of $\pm 2{\cdot}0$ milligal. This figure also represents the total accuracy. The accuracy of the gravity determinations on Marion Island is much less, but this is due to observational errors introduced by the adopted methods.

Absolute Observed Gravity Values

	Date	Longitude	Latitude	Approximate Elevation	Observed Gravity in gals.	Accuracy
Marion Island	7:3:1960	37°51′39″	46°52′34″	40 feet	981·0102*	±4 milligal
					981·0068†	±8 milligal
Tristan da Cunha	21:3:1960	12°17′55″	37°2′46″	75 feet	980·0942	±2 milligal
		12°17′52″	37°2′46″	sea level	980·0981	±2 milligal
Gough Island	23:3:1960	9°53′46″	40°19′16″	15 feet	980·3929	±2 milligal

* Determined by the light beam sensitivity method.
† Determined by the tilt-table method.

For further details about these methods see appendix.

Appendix

Method for extending the operating range of the Worden gravimeter

The Worden gravimeter used had a range of approximately 3,000 milligal and could be operated only to a latitude of 44° south. It was, however, found that this restriction could be overcome by operating the instrument in a tilted position, since it then only measures part of the vertical component of the gravity field. This procedure is analogous to that adopted by the manufacturers for calibrating purposes.

The amount that the reading decreases from the true value depends on the angle of tilt. Theoretically it is possible to extend the upper limit of the instrument's range by an amount equal to the existing range.

A tilt-table was constructed to determine the relation between the tilt and the amount by which the reading deviated from the true value. The tilt was not measured in terms of the angle the instrument made with the horizontal, but was determined at the farthest end of the tilting-beam where a millimetre scale was attached to the base of the tilt-table.

The gravimeter was tilted towards the right, parallel to the beam system, i.e. parallel to the longitudinal levelling bubble while the transverse bubble was kept level. In this way, from a series of observations in various tilt positions, it was determined that the gravitational change due to tilting is a quadratic function of the measured tilt. This deviation, which is the correction that has to be added to the observed gravity value to obtain the true observed gravity value can be calculated from the tilt by the following equation:

$$C = Kt^2 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

Where C = correction in milligal
t = tilt
$K = 4{\cdot}1506$

The constant coefficient K only refers to the particular tilting device used.

Apart from determining the correction C by means of a specially constructed tilt-table, a second and less elaborate method was devised by measuring the sensitivity of the light beam. Since the light beam sensitivity also changes according to the extent that the instrument is tilted, the correction C could be determined from measuring the sensitivity. For this, the gravimeter was tilted to the right by adjustment of the levelling screws.

The beam sensitivity is determined by measuring the number of small dial units that are necessary to move the light beam from the nil line to one of the outside lines. The sensitivity in this case was measured between the nil line and the left-hand outside line. The relation between the beam sensitivity and the correction was determined experimentally from a series of observations in various tilt positions and is illustrated by diagram 2.

For calculating the correction C, the following equation can more conveniently be applied.

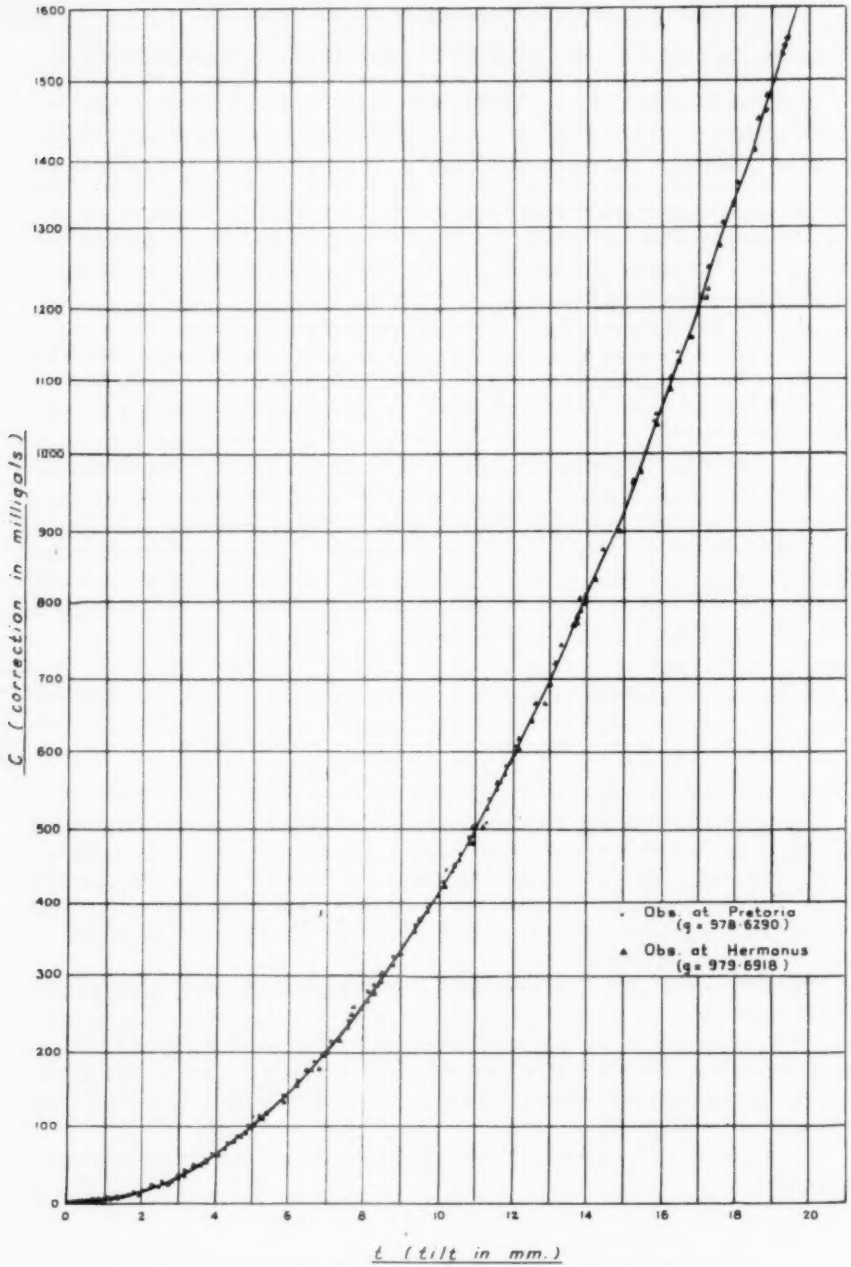


DIAGRAM 1. Graph showing the relation between the correction C and the tilt.
(1 unit of tilt is roughly 9 minutes of arc.)

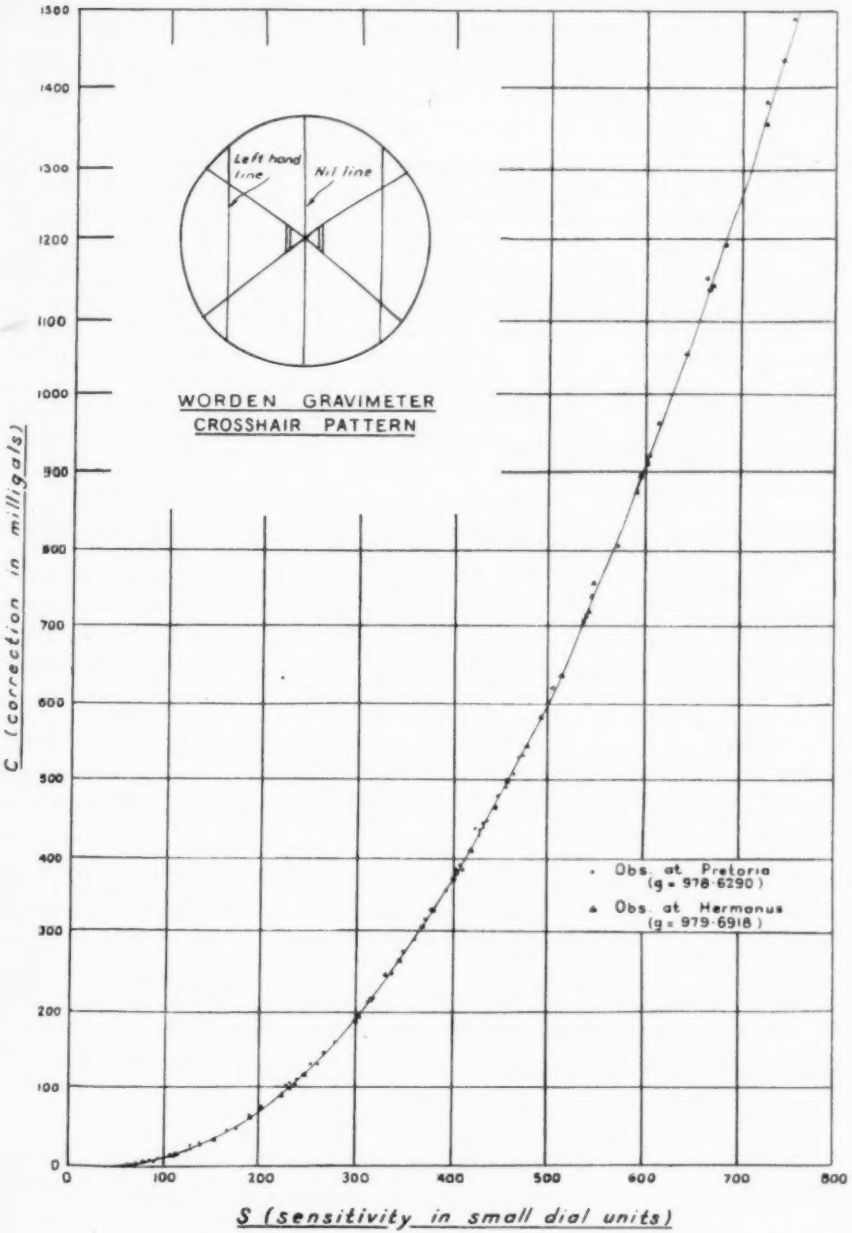


DIAGRAM 2. Graph showing the relation between the correction and the beam sensitivity.

$$C = k(S_t - S_l)^2$$

Where C = correction in milligal
S_t = beam sensitivity in tilted position (measured in small dial units)
S_l = beam sensitivity in level position (measured in small dial units)
$k = 2{\cdot}94 \times 10^{-3}$

Further, the experimental determinations of C, from observations carried out at Hermanus ($g = 979{\cdot}6918$) and Pretoria ($g = 978{\cdot}6290$) indicated that a change in gravity of approximately 1,000 milligal does not affect the value of C within the accuracy that C could be determined. This is illustrated by diagrams 1 and 2 where the observations at Pretoria and Hermanus are plotted separately. Consequently for the determinations of g at Marion, C was considered independent of gravity.

For determining the gravity at Marion both methods were used. The tilt could be measured accurately only to 0·2 millimetres on the tilt-table. In terms of the angle this corresponds roughly to 2 minutes of arc. From equation (1) it can be found that an error of 0·2 millimetres for t can introduce an error of about $\pm 0{\cdot}8$ milligal for every millimetre the instrument is tilted. For Marion Island ($t = 9$ mm.) the accuracy of C is consequently $\pm 7{\cdot}0$ milligal.

The second method concerning the beam sensitivity proved more accurate. At Marion the light beam sensitivity could be determined accurately to 2.0 small dial units which, in this case, involved an error of $\pm 2{\cdot}0$ milligal for C.

The application of these methods, although the results are not very accurate, proved quite useful on this particular survey. It is evident that the procedure is not suitable for accurate work but is merely a means to obtain, during a regional survey, that occasional observation outside the normal operating range of the gravimeter.

ACKNOWLEDGEMENTS

The author wishes to thank the Department of Transport and Director of the Weather Bureau, Pretoria, for the co-operation that made this survey possible, and also Mr. Besaans, Principal Draughtsman to the Geological Survey, and his staff for preparing the text-figures.

TINGIDAE FROM SOUTH AFRICA (HEMIPTERA)

By Carl J. Drake
Smithsonian Institution, Washington, D.C.

(Communicated by A. J. Hesse)

(Read March 15, 1961)

The present paper is based entirely upon a small collection of Tingidae netted by Mr. and Mrs. B. R. Stuckenberg in South Africa. This collection of eight species includes two forms described below as new species. The types are deposited in the Natal Museum. The illustrations were made by Mrs. Patricia J. Hogue, of Arlington, Virginia.

Dictyla picturata (Distant) (Pl. VII)

Monanthia picturata Distant, 1902, *Ann. S. Afr. Mus.*, vol. 2, p. 243, pl. 14, fig. 11.
—Blöte, 1945, *Zool. Mededeelingen*, vol. 25, p. 91.

One specimen: Franschhoek Pass, 7–8.x.1959, figured.

This pretty species is known only from the Union of South Africa.

Cysteochila incolana Drake (Pl. VIII)

Cysteochila incolana Drake, 1956, *Great Basin Naturalist*, vol. 16, p. 18.

2 females and 1 male, Du Toits Kloof, Paarl District, West Cape, 2,000–3,500 feet, 27–28.ix.1959; 4 females, Franschhoek, West Cape, 7–8.x.1959. Originally described from specimens netted in South Africa (Ceres, Cape Town, and Port St. Johns).

Cochlochila capeneri Drake and Slater

Cochlochila capeneri Drake and Slater, 1955, *Acta Ent. Mus. Nat.* Prague, vol. 33, p. 49.

1 male and 2 females, Karoo at junction of Calvinia–Sutherland Road, near Inverdoorn, Ceres, West Cape, 2–3.x.1959; and 1 male and 3 females, Ngome Forest, between Vryheid and Nongoma, Natal, 11–12.iv.1960. Originally described from one female, Rustenburg, South Africa. I also have several specimens from Bedford View, Johannesburg, taken by A. L. Capener.

Paracopium africum Drake

Paracopium africum Drake, 1956, *Philippine Journ. Sci.*, vol. 85, p. 472.

1 male, Nagle Dam, Umgeni Valley, Natal, xii.1959. Known heretofore only from male holotype, Natal.

Habrochila monticola Horvath

Habrochila monticola Horvath, 1929, *Ann. Mag. Nat. Hist.*, Ser. 10, vol. 3, p. 319.

1 male, Deepdale, Umkomaas Valley, Impendhle District, Natal, 7.v.1959. The type specimens were collected near Weenen, Natal, elevation 2,840 feet, 1924.

Agramma onar, sp. nov. (Pl. IX)

Small, slender, smooth. Head, pronotum (save backward projection), antennae, and legs black, slightly shiny; posterior process of pronotum and entire elytra grayish testaceous. Labium blackish, inferior margins of buccal and sternal laminae of labial sulcus brownish testaceous. Length 2·60 mm., width 0·62 mm.

Head convex above, short, strongly deflexed in front, armed with two, short, porrect, brownish or blackish spines; eyes very narrow, blackish. Antennae moderately stout, moderately long, sparsely pubescent, distinctly granulate, measurements of segments: I, 0·15 mm.; II, 0·12 mm.; III, 0·38 mm.; IV, 0·22 mm. Labium extending to middle of mesosternum; sternal laminae of sulcus uniseriate, nearly parallel-sided, open behind. Bucculae wide, closed in front, triseriate. Hypocostal laminae narrow, uniseriate.

Pronotum depressed, punctate, unicarinate, lateral margins nearly straight, slowly converging anteriorly; collum narrow, uniseriate, truncate in front, the posterior projection triangular, areolate. Elytra transversely convex, sides deflected downward; costal area narrow, uniseriate, corium not separated in distinct divisions. Legs short, fairly stout; femora moderately incrassate, constricted at base, longer than tibiae; tarsi moderately swollen. Macropterous form unknown.

Holotype (male), *allotype* (female) and 10 *paratypes*, Cathedral Peak Forestry Reserve, Natal Drakensberg, headwaters of the Indumeni River, elevation 8,500–9,000 feet, March 1959. One of the paratypes has a wide, transverse black fuscous band behind the middle of the left elytron. The other elytron of this specimen and the elytra of the rest of the type series are without any indications of such a transverse band. The male type is illustrated.

Lullius major Distant

Lullius major Distant, 1904, *Trans. S. Afr. Phil. Soc.*, vol. 14, p. 43, pl. 8, fig. 7.

1 male, Karreedouw Mountains, west of Humansdorp, Cape Province, 14.x.1959. Originally described from Cape Colony and known only from South Africa.

Lullius spinifemur, sp. nov. (Pl. X)

Small. Head, pronotum[1] (save backward projection), and body beneath deep black; elytra testaceous with slight brownish tinge. Legs dark reddish to blackish fuscous. Antennae blackish fuscous, third segment becoming brownish apically. Length 2·50–2·75 mm., width (elytra) 0·80 mm.

Head very short, sharply deflexed, armed with a pair of short, porrect, frontal spines. Antennae distinctly granulate, clothed with short, pale pubescence, segmental measurements: I, 0·18 mm.; II, 0·15 mm.; III, 0·70 mm.; IV, 0·23 mm. Bucculae wide, triseriate, closed in front. Labium extending on prosternum; rostral laminae of sternal sulcus low, uniseriate, open behind. Hypocostal laminae narrow, uniseriate, tapering posteriorly.

Pronotum subdepressed, distinctly punctate, unicarinate, truncate in front, with lateral sides before humeri slowly obliquely narrowed anteriorly, backward projection

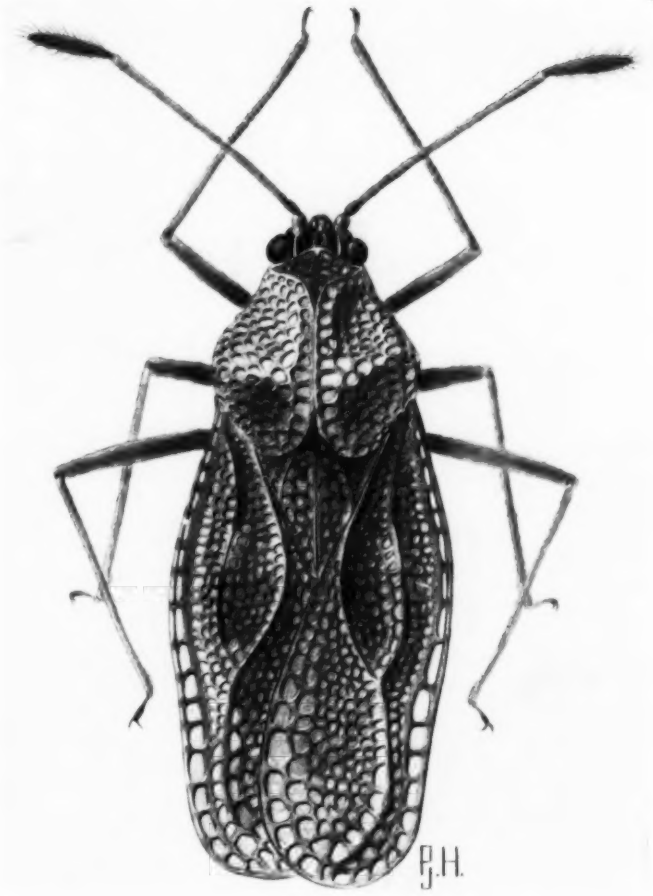
of hind margin triangular. Elytra with division of corial area not clearly defined, longer than abdomen, with exterior sides strongly deflected downwards so as to cover completely sides of abdomen, exterior margin distinctly rounded (Pl. X); costal area narrow, uniseriate; discoidal area large, boundary veins separating it from subcostal and sutural area scarcely indicated.

Legs fairly stout, short, sparsely provided with short, pale pubescence; femora moderately swollen, strongly constricted at base, longer than tibiae; tarsi moderately incrassate, second segment beneath depressed, and provided with numerous, short, pale, setal-like hairs. Each femur, both male and female, armed on inferior side just beyond the basal constriction with a prominent spine, which is longer in male than female; femoral spine of fore femur (male) longer than that on middle femur, represented by a small tubercle on hind femur; femora of female provided with shorter spines on fore and middle legs, tubercles on hind femora scarcely discernible. Spines in the same relative position on all three pairs of legs in both sexes.

Holotype (male) and *allotype* (female), Sevenweekspoort, Laingsburg District, West Cape Province, 19–22.ix.1959, collected by Mr. and Mrs. B. R. Stuckenberg.

This is the second species of the family Tingidae described with spines on the legs. The spines are paired, one near the base of each femur of fore and middle legs and replaced by a tiny tubercle on each hind leg. The spines are distinctly larger in male than in female. The ♀ allotype is illustrated from lateral aspect; and fore femur of male to show spine.

The genus *Lullius* Distant (1904) differs largely from *Agramma* Stephens (1829) in having the elytra strongly deflected on the sides so as to conceal the abdomen in profile. The tibiae are shorter than the femur. Mr. R. J. Izzard has kindly checked the type species of the genus, *Lullius major* Distant from South Africa, for me and states that the femora are without spines. The femoral spines modify the present conception of unarmed legs in the family Tingidae.



Dictyla picturata (Distant).

Cysteochila incolana Drake.

Agramma onar, n. sp.

Lullius spinifemur, n. sp.; *a*, ♀ lateral aspect; *b*, male fore femur showing subbasal spine at constriction.

TWO NEW SPECIES OF SALDIDAE FROM SOUTH AFRICA (HEMIPTERA: SALDIDAE)

By Carl J. Drake
Smithsonian Institution, Washington, D.C.

(Communicated by A. J. Hesse)

(Read March 15, 1961)

The present paper is based upon shorebugs of the Family Saldidae, collected by Mr. and Mrs. B. R. Stuckenberg in South Africa. This collection contains three species, two of which are described herein as new. The types of the new species are in the Natal Museum. The illustrations were made by Mrs. Patricia J. Hogue of Arlington, Virginia.

Saldula ripa sp. nov. (Pl. XI)

Macropterous form: Large, black, slightly shiny, rather densely clothed with very short, tiny, grayish yellow or yellowish pubescence, the embolium, one or two spots in clavus, five or six spots in corium, apical callosities on front of head yellowish, brownish or whitish testaceous; body beneath blackish, slightly shiny, abdominal sterna blackish fuscous with hind margins of segments brownish; acetabula mostly whitish or brownish; antennae brownish black, with inferior surface of first two segments pale, the pubescence short, inconspicuous. Legs dark brownish fuscous, with superior surface of hind femora towards the base, inferior surfaces of all femora, trochanters, and coxae pale brown or brownish testaceous; pubescence very short, brownish, and inconspicuous; tibiae sparingly provided with short spinulae. Length 5·40–5·60 mm., width (hemelytra) 2·25 mm.

Head strongly deflexed, with median longitudinal furrow; transocular width 1·38 mm.; apical callosities on front whitish testaceous, or dark and then difficult to see, the paired callosities on vertex pale testaceous or concolorous with vertex and then scarcely visible; ocelli very small, separated from each other by slightly more than diameter of an ocellus, with a line connecting antero-inner notches of the excavations of the eyes barely touching the bases of the ocelli. Labium brownish fuscous, shiny, extending between bases of hind coxae. Antennae long, without long hairs, segmental measurements: I, 0·48 mm.; II, 1·72 mm.; III, 1·00 mm.; IV, 1·00 mm.

Pronotum obliquely narrowed anteriorly, twice as wide at base as across collar (160:72), width at base 2·00 mm., median length 0·45 mm.; callus large, moderately raised, not extending outward on explanate margins, with moderately large discal fovea (sometimes with a smaller impression on each side of it) set off by furrows each with a row of small pits in bottom; explanate margins moderately wide, with exterior edge forming a nearly straight line (feebly sinuate); hind lobe one-half as long as callus, the hind margin widely concavely excavated. Scutellum slightly

convex, scarcely wider at base than median length, divided at middle by a transverse furrow, without transverse ridges, the surface and vestiture as on pronotum.

Hemelytra wider and longer than abdomen, markings and divisions as shown in illustration; membrane dark fuscous, with veins blackish. Hind tibiae very long, straight, the spines short, not numerous. All tarsi with second segment slightly shorter than third. Hind wings well developed, transparent. Female with seventh abdominal sternum longer than preceding segments.

Holotype (male) and *allotype* (female), and 5 paratypes, Umgeni Valley, Bothas Hill, Natal, South Africa, x.1958, collected by Mr. and Mrs. B. R. Stuckenberg.

This species belongs with the larger members of the genus *Saldula* Van Duzee described from southern and central Africa. It differs from those species as follows: *S. Machadoi* Drake from Angola has shorter antennae, hairy legs, and the dorsal surface of pronotum and hemelytra clothed with long, erect hairs; *S. africana* Drake from Uganda and South Africa is similar in colour and markings, but the dorsal vestiture is composed of moderately long hairs and the hind tibiae are slightly bowed; and *S. capicola* Drake from South Africa has the dorsal surface dull (not shiny like other species above), short pubescent hairs on hemelytra, hind tibiae slightly bowed, and tarsi of both middle and hind legs much slenderer. The rest of the species known from South Africa are distinctly smaller, including the new species below.

Saldula lita sp. nov. (Pl. XII)

Small, obovate. Head, pronotum, and scutellum deep black, shiny, the two pairs of callose spots on vertex whitish testaceous; hemelytra not as black as pronotum, scarcely shiny, embolium and corium and clavus conjoined, with around ten, small, rounded, whitish or yellowish spots, the membrane infuscated, composed of four cells, with pale marks as shown in the illustration. Body beneath black, slightly shiny, clothed with grayish pubescent hairs. Legs brownish fuscous, with femora largely blackish fuscous, hind tibiae above brownish testaceous. Dorsal surface clothed with very short, small, yellowish or grayish pubescence. Legs with short, brownish pubescence, hind tibiae with several moderately long, dark fuscous spinulae. Antenna with short, brownish pubescence. Labium long, fuscous, shiny. Length 3·30 mm.; width (hemelytra) 1·50 mm.

Head strongly declivent, median furrow distinct in front of ocelli, width across eyes 1·00 mm.; ocelli moderately large, separated from each other by less than diameter of an ocellus, location such that an imaginary line connecting antero-inner ends of excavations of eye passes through bases of ocelli; three pairs of trichobothrial hairs moderately long, the middle and hind pairs originating from pale, callous spots. Antennae rather short, segments III and IV subequal in length, either segment subequal to width of vertex across ocelli, segment II one-half as long as transocular width (40:80) at ocelli, segmental measurements: I, 0·31 mm.; II, 0·50 mm.; III, 0·38 mm.; IV, 0·38 mm. Labium extending between hind coxae.

Pronotum much wider at base than medium length (110:30), with hind margin broadly excavated; strongly narrowed anteriorly, with outer edge of explanate

margin forming a moderately convex line, collar much narrower than transocular width; callum large, moderately elevated, with a large discal fovea, not extending outwardly on explanate margins, set off by the usual transverse, sinuate furrows (one row of tiny pits in bottom of each); hind lobe shorter than callus (15:20). Scutellum with median length and basal width subequal (70:70), with the shallow, transverse impression slightly above the middle.

Hemelytra (macropterous) slowly convexly narrowed beyond middle; membrane with four long cells. Tarsi with second segment scarcely longer than third. Hind tibiae straight. Female and brachypterous forms unknown.

Holotype (male), Stormsriver Pass, Tsitsikama Range, indigenous forest, 12–13. x.1958.

The form, size, hemelytral markings, and the short antennae (including segmentation) distinguish this species from the other new species. The illustration shows the location of the pale markings on the hemelytra.

Saldula ripa, sp. nov. (Holotype)

Saldula lita, sp. nov. (Holotype)

THE WATER ECONOMY OF THREE SPECIES OF THE AMPHIBIOUS CRAB, *POTAMON*

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(Read August 17, 1960)

1. The rate of water loss in air from three species of the fresh-water crab *Potamon* has been determined at various relative humidities and a constant temperature of 20° C. Water is lost, not only from the gill cavity but also through the integument. The rate of water loss decreases with desiccation. This decrease is probably due to decreasing permeability of the integument as desiccation progresses.

2. Of the three species studied, *P. sidneyi* has the lowest rate of water loss. There is no significant different between the rate of water loss of *P. depressus* and *P. warreni*. Evidence is presented that this greater resistance of *P. sidneyi* to desiccation is not due to a difference in permeability of the integument.

3. The survival time and the water loss at death have been determined for all three species. The lethal water loss is the same in all conditions of desiccation studied. *P. sidneyi* has a higher lethal water loss than the other two species. This, together with its lower rate of water loss, results in it having a longer survival time in dry air than the other species.

4. The lethal water loss of *Potamon* is low compared with most other terrestrial arthropods. Death is due to water loss and not to asphyxiation following desiccation of the respiratory surfaces.

5. *Potamon depressus*, when offered a choice, prefers a more humid environment. The intensity of the preference shown is affected both by the magnitude and absolute value of the gradient offered.

6. Evidence suggests that the intensity of the humidity preference of fully hydrated *P. sidneyi* is less than that of *P. depressus* or *P. warreni*.

7. The percentage of time spent in water by crabs offered a choice of water or 'land' has been determined. *P. sidneyi* spends more time in the water than do the other two species. In conditions of alternating light and dark, *P. sidneyi* spends relatively more time in water during the light periods: the behaviour of the other two species is not affected by this factor.

8. The rates of water uptake, following desiccation, of normal and eyestalkless *Potamon sidneyi* have been compared. In winter removal of the eyestalks increases the rate of water uptake: in summer it does not. The rate of water uptake of normal summer crabs is similar to that of eyestalkless winter crabs.

9. The water drive of eyestalkless winter crabs is probably less than that of normal crabs.

In the invasion of the land two pathways have been open to aquatic animals: the one directly from the sea by way of the littoral zone, the other from the freshwaters. The crustacea, apart from the isopods, have been relatively unsuccessful in establishing themselves on land. Many of the Decapoda are, however, partly terrestrial in habit. The majority of these are littoral forms and their adaptations to terrestrial life have been fairly extensively studied. Far less is known of those few freshwater decapods which are amphibious in habit. Of these the genus *Potamon* is one and it appeared of interest to obtain information upon the terrestrial adaptations, and especially the water economy, of this genus.

Potamon is found widely distributed throughout Africa where it is represented by a very large number of species. Three of these occur in the river systems of Natal,

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namely *P. sidneyi* Rathbun, *P. warreni* Calman and *P. depressus* (Krauss). A comparative study of their degree of terrestrial adaptation seemed of value for the light it might throw upon their distribution and their relative abilities to migrate from one river system to another.

The observations which follow are preliminary, but unfortunately both authors had to leave Natal before they could be completed. It was felt, however, desirable to place them on record for comparison with other amphibious decapods.

I. DESICCATION

Materials and Methods

Animals collected in the field were kept in the laboratory in large aquarium tanks filled with sufficient water just to cover the crabs. The animals were fed weekly on raw steak which was generally readily accepted. They appeared to live healthily in these conditions.

To study rates of water loss, desiccation chambers made of deep beakers were used. The diameter of the beaker was adequate to contain the crab, but too small to permit much movement. Compressed air, of controlled humidity, was led into the bottom of each beaker and passed upwards at a speed of 0·02 cm./sec. through a series of baffle plates. The crab rested on the top baffle plate and the beaker was closed with a perforated lid. All experiments were conducted at 20° C.

Before an experiment the crabs were moved into individual glass jars containing sufficient water almost to cover them. They were allowed three days to adapt to these conditions at 20° C. before being used for experimental purposes: during this period they were not fed. At the beginning of an experiment the animals were drained of water, dried in a soft towel to remove free water from the external surfaces and then weighed. The first weight will be referred to as the initial weight.

The Rate of Water Loss of P. depressus

P. depressus is the most readily obtainable of the three species of crab and, for this reason, has been studied most intensively. Its rate of water loss was determined at 30% and 78% relative humidity (R.H.). At 30% R.H. nine animals of a mean initial weight of 34·2 g. were used and at 78% eight animals of mean initial weight 20·1 g. The results obtained are shown in figure 1. It will be seen that in both cases there is a rapid initial loss of water, but that this high rate rapidly falls to a fairly low and constant value. The question immediately arises as to whether this fall in the rate of water loss is due to an active control of the process by the animal. Zoond and Charles (1931) have suggested that there might occur, on the gills of *Potamon*, glands which secrete a substance which serves to reduce the water loss across the gill surfaces.

To investigate this point a study was made of the rate of water loss of live and dead crabs. The animals used were killed by the injection of a normal solution of

potassium cyanide at a dosage level of 1 ml/100 g. body weight. The injection was made into the stump of an autotomized limb. Following the injection the animals were left in a dry dish to die. This invariably occurred within five minutes.

Control animals were treated in identical fashion, but were injected with a similar dose of normal sodium chloride solution. This appeared to have no deleterious effect upon the animals. Both groups were weighed at regular intervals and the experiment continued for some hours after the living animals had died, in case death should be accompanied by a marked change in the rate of water loss.

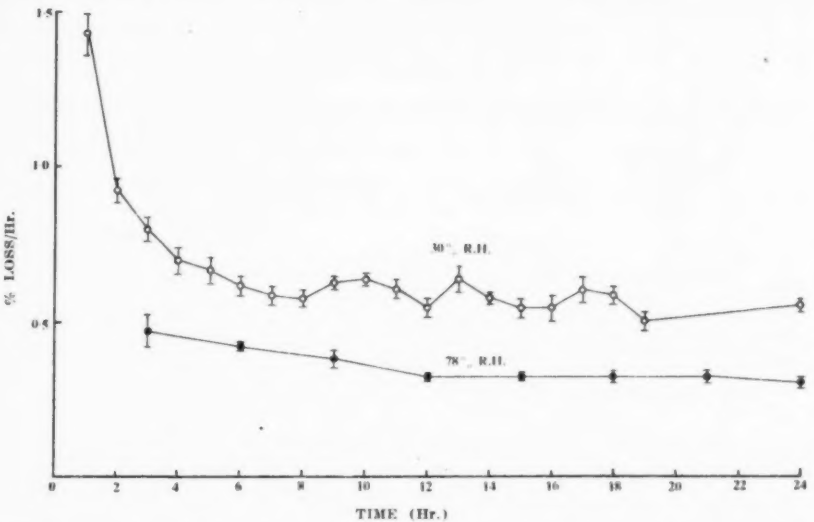

FIG. 1. *Potamon depressus*. Water loss as a percentage of initial weight at intervals after the onset of desiccation. Open circles, mean of nine animals at 30% R.H.; closed circles, mean of eight animals at 78% R.H. In this and subsequent figures, vertical lines indicate twice the standard errors of the observations at each point.

This type of experiment was made at both humidities. As far as possible the weights of the experimental animals and their controls were similar. At 30% R.H. twelve experimental and six control animals were used; the mean initial weights of the two groups were 35·0 and 40·1 g. respectively. At 78% R.H. six experimental and nine control animals were used: the mean initial weights were 18·7 and 20·0 g. respectively. The results obtained are shewn in figure 2. It is apparent that there is no striking difference between the rates of water loss of living and dead crabs. There is however one possibility worth further consideration. It might be that on exposure to air there is an immediate secretion of protective material over the surface of the gills. Such an event, if sufficiently rapid, would occur in both control and experimental groups in the present experiments. No histological evidence for such secretory structures has been found, but the possibility has not been finally excluded.

Further examination of the results obtained at 78% R.H. shews that the rate of water loss of dead animals is actually lower than that of living ones. This effect has also been observed in *Ligia exotica* (Numanoi, 1934), and in *Carcinides moenas* (Lafon, 1948). Both Numanoi and Lafon suggest that the movement and metabolism of the living animals are responsible for this result. Certainly the living *Potamon* moved restlessly during the desiccation experiments and this may have facilitated the movement of air around the body. A further contributory factor may be that the maintained circulation in a living animal will tend to increase the water loss from the gills since fresh blood will constantly be brought to these surfaces.

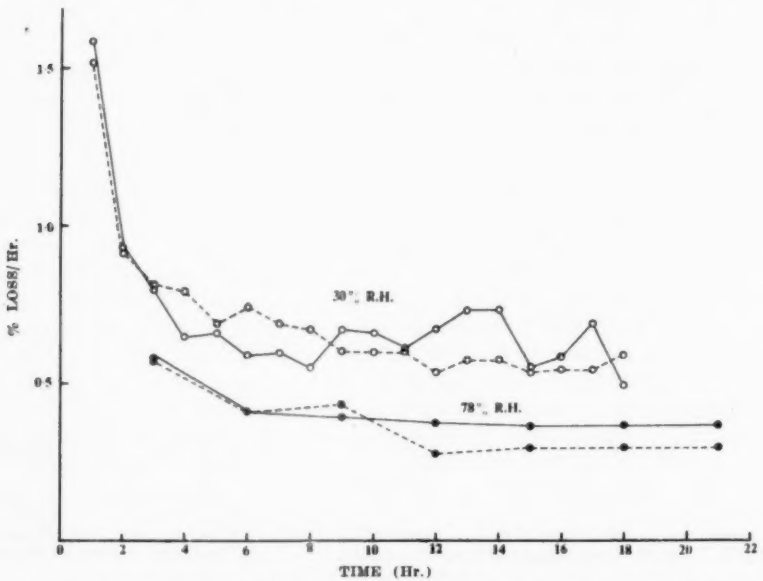

FIG. 2. As fig. 1. Comparison of water loss of live and dead crabs. Open circles, 30% R.H.; closed circles, 78% R.H. Full line, living animals; broken line, dead animals.

It thus appears that there is no compelling evidence to support the view that any active control of water loss is present in *P. depressus* and that the explanation of the high initial rate of water loss must lie elsewhere.

THE SITE OF WATER LOSS

In the preceding discussion it has been tacitly assumed that the main site of water loss is from the gills. Before proceeding further, it appeared desirable to test the validity of this assumption.

For this purpose certain areas of the crabs were sealed by covering them with a thick solution of 'Duco'. Since such operations were found impractical with living

animals, all experiments were made on crabs which had been killed by an injection of cyanide. Three different areas were recognized for this experiment, namely (i) the general integument, (ii) the 'tail area' beneath the ventrally flexed abdomen including the pleopods and (iii) the branchial surfaces. All animals used were females.

Five animals were included within each group and five control animals were also used. The initial weight of all animals was within the range of 20–30 g. The rate of water loss over a period of 24 hr. at 20% R.H. was determined for each group. It is assumed that any observed decrease in water loss compared with that of the controls is a measure of the normal rate of loss from the occluded surface. The results of these experiments are summarized in Table I.

TABLE I

Rates of water loss from *Potamon depressus* with different regions of the body occluded by 'Duco'

Area occluded	Rate of water loss		Calculated % loss through occluded area
	As % of original weight per 24 hr.	As % of loss by controls	
None	14·70	100·0	0·0
Integument	8·70	59·2	40·8
Branchial chambers	10·50	71·4	28·6
Tail area	12·20	83·2	16·8
		Total	86·2

It will be seen that about 40% of the water loss appears to occur through the general integument, slightly less than 30% from the branchial cavity and just over 15% from the 'tail region'. However the values in the final column do not total the expected 100%. This is probably partly due to the small number of animals used in each experiment and partly to the difficulty of effecting a complete occlusion of the branchial cavities: a slow loss of weight by the 'Duco' may also contribute to the discrepancy. The results therefore probably tend to underestimate the contribution from these cavities which may be as great, or possibly greater than, the loss through the general integument.

It is, however, clear from these experiments that the general integument is as important a site of water loss as the branchial cavities. A similar effect has been found in *Armadillidium*, *Porcellio* and *Ligia* (Edney, 1951) where it has been shown that water loss across the respiratory surfaces represents only about one-third of the total.

It has been suggested above that the initial hyperbolic portion of the desiccation curve is not due to any active control of water loss by the crab. It might be due to a relatively rapid rate of loss of adventitious water from arthrodial membranes, mouth parts and the branchial cavities. However, the demonstration of the importance of the general body surface in water loss raises the possibility that the process of desiccation may reduce the permeability of the integument and thus lower the rate of water loss. Such an effect has been found in *Oniscus ascellus* by Bursell (1955).

To test this possibility the variation in the rate of water loss with time was determined in a series of nine experimental animals in which the tail area and the branchial cavities had been sealed off with 'Duco': ten animals were used as controls. All animals were initially killed by an injection of cyanide. The results obtained are summarized in Table II. It will be seen that in both groups there is a rapid loss of weight during the first two hours, but that after that the loss rate falls only slowly with time. Since in the experimental animals the major surfaces from which adventitious water might be lost were occluded, it seems reasonable to conclude that, in part at least, the hyperbolic nature of the desiccation curve arises from a change in the water permeability of the exoskeleton as it dries: the loss of adventitious water as a contributory element in the effect is not however excluded.

TABLE II

Comparison of rates of water loss, expressed as percentage weight loss/hr., by normal *P. depressus* and individuals with only the integument exposed

Hour of experiment	Experimental	Control
1st	1·66 ± 0·11	1·45 ± 0·07
2nd	0·95 ± 0·04	1·13 ± 0·05
3rd	0·75 ± 0·05	1·13 ± 0·04
4th	0·75 ± 0·04	0·98 ± 0·03
5th	0·69 ± 0·04	0·82 ± 0·03
6th	0·64 ± 0·05	0·83 ± 0·04
7th	0·60 ± 0·03	0·76 ± 0·04
Mean initial weight (g)	24·63	24·60

THE RELATIVE RATES OF DESICCATION OF THE THREE SPECIES OF POTAMON

While *P. depressus* is abundant, *P. sidneyi* is less readily collected and *P. warreni* is scarce. It was therefore necessary to use animals from different weight classes to make an effective comparison between the three species. The animals were grouped in arbitrary classes by their carapace width, as measured between the epibranchial corners. Each class covered specimens within an interval of 0·5 cm. of carapace width. Desiccation was effected at 25% R.H. and continued over a period of 12 hrs. Hourly weighings shewed that in all species the rate of water loss had become constant after six hours and the results presented compare the rates from the sixth to the twelfth hour of desiccation. In each size class twelve specimens of *P. depressus* and six of *P. sidneyi* were used. Equal numbers of the two sexes were used in each size group. The results obtained with *P. warreni* are presented as individual observations as only six specimens in all were available.

The results of these experiments are summarized graphically in figure 3. It can be seen immediately that the rate of water loss of *P. sidneyi* is significantly less than that of *P. depressus* for all size groups except the two smallest. In the largest crabs the rate of water loss of *P. sidneyi* is about 80% of that of *P. depressus*. The results

further suggest that the rate of water loss of *P. warreni* is of the same order as that of *P. depressus* and definitely higher than that of *P. sidneyi*. Using over-all mean rates of water loss up to death, that is including the hyperbolic portion of the desiccation curve, this difference in rate of water loss between *P. sidneyi* and *P. depressus* has also been found at 50% and 70% R.H.; at 90% R.H. the difference is not significant. The results of these measurements are shewn graphically in figure 4. It will be seen that in all three species there is an almost linear relation between the over-all mean rate of water loss and the saturation deficit. Such variations as occur within a species

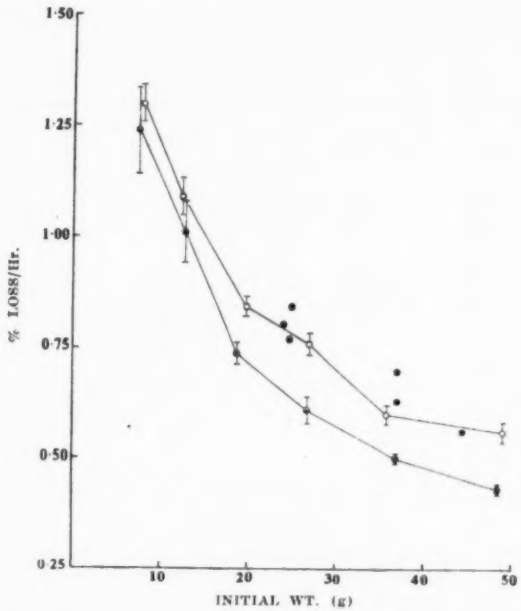

FIG. 3. Rates of water loss, as percentage of initial weight lost per hour, for different size groups of three species of *Potamon*. o *P. depressus*; • *P. warreni*; ⊕ *P. sidneyi*

can be shown to be due to variations in the mean weight of different batches of crabs. Thus in the curve for *P. depressus* the mean weights of those animals used at the two lowest humidities were significantly greater than those used at higher humidities.

The results obtained also show that the rate of water loss per unit initial weight decreases with increasing size. This is to be expected as the surface/volume ratio will decrease with increasing size. A similar effect has been shewn with *Carcinides* by Lafon (1948). It can be expressed by the relationship $r = kW^x$, where r is the rate of water loss, k is a constant dependent on the permeability of the surfaces,

W is the weight of the animal and x is a factor expressing the relation of surface to weight. The determination of these values gives the following results: x is 0·45 for *P. sidneyi* and 0·52 for *P. depressus*, while k is 3·6 for *sidneyi* and 3·5 for *depressus*. These figures suggest that a difference in permeability of the integument and gill surfaces is not a factor which causes the lower rate of water loss of *P. sidneyi*. The main factor producing the difference is reflected in the value of the exponent x, suggesting that some geometrical difference in body form, or possibly in the openings of the branchial cavities, gives *P. sidneyi* greater protection than *P. depressus*. The data given in figure 3 shew further that this difference becomes more marked with increasing size.

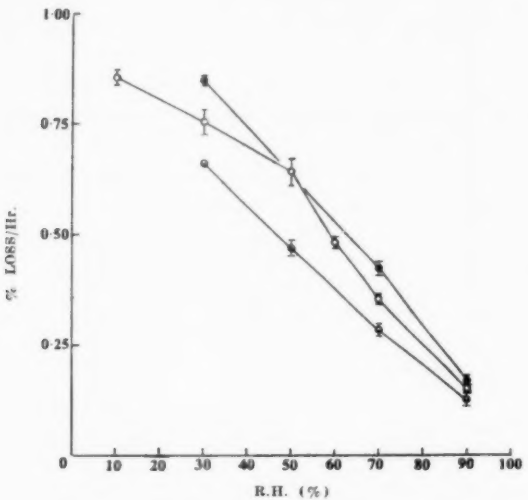

FIG. 4. Rates of water loss of three species of *Potamon* at different humidities. o *P. depressus;* ● *P. warreni;* ⊖ *P. sidneyi.*

THE SURVIVAL TIME OF THE THREE SPECIES DURING DESICCATION

The resistance of an animal to water loss is not only a function of the rate at which water is lost, but also of the total water loss which can be tolerated. Thus of two animals which lose water at the same rate, the one that can withstand the greater total water loss is clearly the better adapted to withstand transient desiccations. The survival times of the three species of *Potamon* have therefore been studied in controlled conditions of humidity and air flow. Animals were desiccated and observed at hourly intervals. They were assumed to be dead if they displayed no movement when stimulated. The weight loss at the time of death was noted and this, expressed as a percentage of the initial weight, will be referred to as the lethal weight loss (L.W.L.).

A preliminary experiment was made with *P. depressus* to ensure that the drying agent used was having no effect upon the results. The L.W.L. was determined at 10% R.H. using calcium chloride, potassium hydroxide and sulphuric acid as drying agents. No significant differences were found between the L.W.L. for the three groups of animals exposed to air which had passed over the three different drying agents. In all subsequent experiments calcium chloride was used as drying agent. The first point to be investigated was the effect of size upon survival time and L.W.L. Three groups of *P. depressus*, characterized as large, medium and small, were used. The desiccations were effected at 10% and 70% R.H. The results obtained are shown in Table III. It can be seen that the survival time at both humidities is

TABLE III

Survival time and lethal water loss of three size groups of *Potamon depressus*

Size group	R.H. (%)	No. of animals	Initial weights (g)	Survival time (hr.)	L.W.L. (%)
Large	10	5	35·3–40·6	19·8 ± 0·8	16·09 ± 0·67
Medium	10	7	23·3–29·4	18·3 ± 0·9	15·45 ± 0·48
Small	10	5	11·8–15·2	13·5 ± 1·5	16·02 ± 0·97
Large	70	4	37·0–47·5	52·8 ± 4·0	15·24 ± 0·77
Medium	70	7	19·3–26·0	41·7 ± 3·7	14·57 ± 0·87
Small	70	4	12·9–14·3	36·0 ± 1·7	15·73 ± 0·74

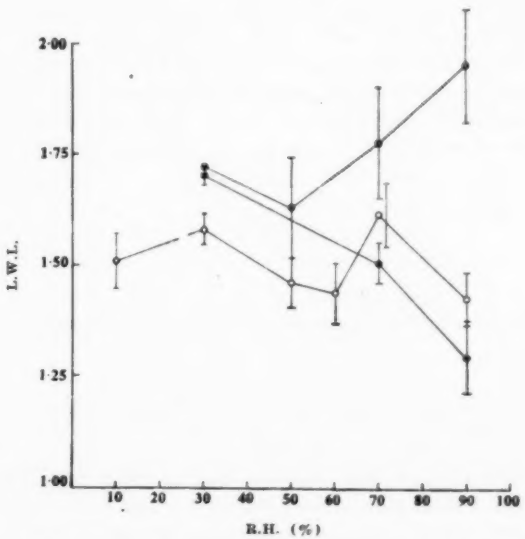

FIG. 5. Lethal water loss of three species of *Potamon* at different humidities. o *P. depressus*; • *P. warreni*; ◒ *P. sidneyi*.

markedly affected by weight. A similar effect is reported by Pearse (1929) using *Ocypode albicans* Bosc. and *Calcinus sulcatus* (H. M-Edw.). On the other hand the L.W.L. is almost constant; even the most extreme differences found are not statistically significant. The difference in survival times is therefore to be attributed simply to differences in rates of desiccation which, as shewn previously, are relatively lower in larger animals.

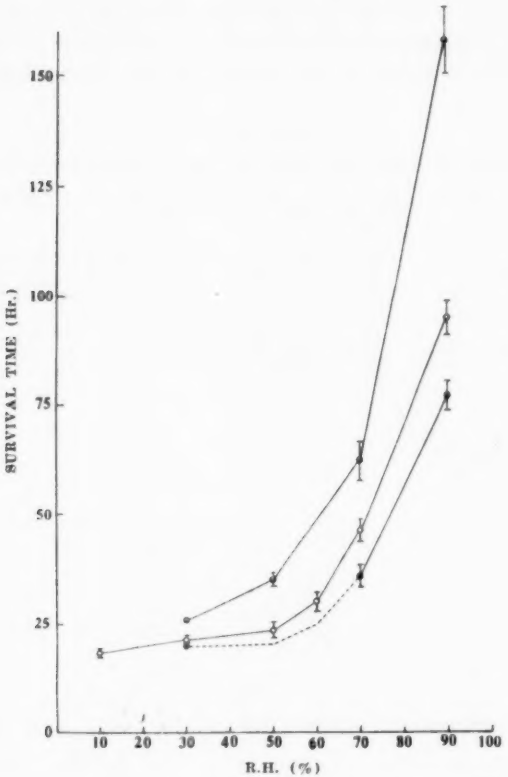

FIG. 6. Survival times of three species of *Potamon* at different humidities. o *P. depressus*; • *P. warreni*; ⊖ *P. sidneyi*.

The results also indicate that humidity has no effect upon the L.W.L. This point was examined further over a more extensive range of humidities. The results obtained are shewn in figure 5. Again no evidence for any effect of the desiccating humidity upon the L.W.L. was found, nor was there any evidence of a difference in L.W.L. between the sexes. Figure 5 also summarizes data on the L.W.L. of *P. warreni* and *P. sidneyi*. It will be seen that there is no clear trend in these observations. The

values for the L.W.L. for *P. sidneyi* at different R.H.s are not significantly different from one another (maximal value of $t = 0{\cdot}79$). There is therefore no reason to assume that in this species the L.W.L. is influenced by the humidity at which desiccation has been effected. At 30% R.H. the difference between *P. depressus* and *P. warreni* is not significant ($t = 0{\cdot}56$), but at 90% R.H. the difference between *P. sidneyi* and the other species is highly significant ($P < 0{\cdot}01$). This suggests that the L.W.L. of *P. sidneyi* is indeed greater than that of the other two species, but that the relatively small size of the groups of crabs used resulted in such great variance as to conceal the effect at lower humidities.

If survival time is considered the combined effects of its lower rate of water loss and its rather greater tolerance towards this water loss act together so as to separate *P. sydneyi* clearly from the other two species. This is shewn in figure 6. The differences between *P. sidneyi* and *P. depressus* shewn here are all significant ($P < 0{\cdot}01$), those between *P. depressus* and *P. warreni* are of doubtful significance ($P < 0{\cdot}05 > 0{\cdot}02$). It would therefore appear that *P. sidneyi* is better adapted to withstand desiccation than either *P. warreni* or *P. depressus*.

Specific differences in L.W.L. and the cause of death from desiccation

The specific differences in L.W.L. might arise in a number of different ways. The first to be considered stems from the way in which L.W.L. has been expressed, namely as a percentage loss of total weight at death. If, in *P. depressus*, the exoskeletal structures contribute a greater proportion to the total weight than in *P. sidneyi*, then clearly the latter could tolerate a greater absolute water loss for it will have an initially higher water content. However, estimates of the total water content of all three species shew there to be no significant difference between them (Table IV): indeed, if anything *P. depressus* has a higher initial water content than *P. sidneyi*.

Table IV

Total water content of three species of *Potamon*

Species	Number of observations	Water content as % of initial weight
P. depressus	36	$68{\cdot}42 \pm 0{\cdot}77$
P. sidneyi	20	$65{\cdot}68 \pm 0{\cdot}95$
P. warreni	8	$65{\cdot}79 \pm 1{\cdot}40$

Note: There is no indication of a correlation between size and water content in any species. The difference between the water contents of *P. depressus* and *P. sidneyi* is not clearly significant. $t = 2{\cdot}14$; $P < 0{\cdot}05 > 0{\cdot}02$.

In considering this problem further it is of interest to compare the L.W.L. values of *Potamon* with those of other invertebrates. An abstract of some of the results obtained by other authors is given in Table V. It will be seen that the L.W.L. of *Potamon* is strikingly lower than that of other, almost all tracheate, forms. This

suggests that while death from desiccation in a tracheate organism is due directly to water loss, death in similar conditions in a gilled animal like *Potamon* might be due to asphyxiation, the desiccation of the gills rendering them useless for oxygen exchange. Such indeed appears to be the case in the woodlice *Ligia*, *Oniscus* and *Porcellio* (Edney and Spencer, 1955) where the L.W.L. varies directly with the rate of desiccation. It might then be that the specific differences in L.W.L. arise from differences in the relative rates of water loss, the slower rate of water loss by *P. sidneyi* delaying the onset of a lethal anoxia.

TABLE V

Water contents and lethal water losses of different invertebrates

Species	Total water content (%)	Lethal water loss as % total water content	Lethal water loss as % body weight	Authority
OLIGOCHAETA				
Allolobophora chlorotica	80	>75	>60	Roots (1956)
Lumbricus terrestris	85	>70	>60	Roots (1956)
CRUSTACEA				
Ligia oceanica	73	40	29	Lafon (1948)
Porcellio scaber	69	>24	>16·5	Auzou (1953)
Oniscus ascellus	72	31	22	Auzou (1953)
Potamon depressus	68	22	15	This paper
Potamon sidneyi	66	27	18	This paper
Potamon warreni	66	23	15	This paper
ONYCHOPHORA				
Peripatopsis moseleyi	—	—	>33	Dodds and Ewer (1952)
DIPLOPODA				
Orthomorpha gracilis	—	—	>40	Perttunen (1953)
Schizophyllum sabulosum	—	—	>40	Perttunen (1953)
Julus terrestris	—	—	>40	Perttunen (1953)
INSECTA				
Blatta orientalis	77	54	42	Gunn (1933)
Chortophaga viridifasciata	76	58	45	Ludwig (1937)
Rhodnius prolixus	—	>55	>40	Buxton (1932)
Cimex lectularius	—	45	30	Mellanby (1932)
Popillia japonica (larva)	81	69	56	Ludwig and Landsman (1937)
Tenebrio molitor (larva)	—	—	>20	Hall (1922)
Tenebrio molitor (adult)	—	—	>30	Pielou and Gunn (1940)
Xenopsylla cheopis	—	—	>50	Bacot and Martin (1924)

In *Potamon*, however, unlike the isopods, we have already seen that the L.W.L. is independent of the rate of desiccation. (Fig. 5.) As a further test, a set of experiments were made in which the L.W.L. of crabs whose carapace had been heavily coated with vaseline was determined. It would be expected that, if death were due to anoxia following dehydration of the respiratory surfaces, this treatment should result in a fall in the L.W.L. The results of these experiments are set out in Table VI.

It will be seen that there is no marked difference between the L.W.L. of the control and of the experimental series ($P > 0{\cdot}10$), but the survival times of the experimental series are more than twice those of the controls, a result which would be expected if water loss itself were the cause of death.

TABLE VI

Effect of covering the carapace of *P. depressus* with vaseline on rate of water loss, lethal water loss and survival time at 10% R.H.

	Mean initial weight (g)	No. of specimens	L.W.L. % of initial weight	Survival time (hr.)	Mean rate of water loss (% hr.)
Experimental	25·4	11	14·50	51	0·29
Control	23·3	6	16·04	21	0·77

The greater L.W.L. of *P. sidneyi* could arise from the tissues of this crab having a greater tolerance to high osmotic pressure than have those of *P. depressus*. This possibility, however, has not been investigated.

II. RESPONSES TO HUMIDITY

METHODS

During preliminary experiments designed to study humidity preferences, choice chambers similar to those described by Gunn and Kennedy (1936) were used. While the results obtained shewed that the crabs will respond to humidity, it was soon apparent that it was impossible to maintain in the chambers any particular humidities. Edney hygrometers placed in the chambers together with single crabs indicated that a micro-climate of high humidity develops in the region around the animal. To obtain a clearer picture of the extent and character of the response to humidity, the conditions must be controlled and maintained constant. To meet this requirement a method initially designed by Poynton (1954) for similar work on frogs was used. This retains the principle of the choice chamber but incorporates an airflow system so that a microclimate cannot build up around an animal. In effect the animals are offered a choice between two air streams of different humidities.

The choice chambers were glass dishes 26 cm. in diameter and 13 cm. deep. Two streams of compressed air were led to the bottom and opposite sides of each chamber. The air then passed upwards through a series of baffle plates which broke up the initial jets and gave a uniform airflow across the section of the chamber. The baffles were supported by a solid vertical partition which also divided the lower part of the chamber and kept separate the two airstreams. Above the baffles and 6 cm. from the top of the chamber rested a false floor of perforated zinc sheet. Lids for the chambers were provided by circles of clear glass through which were drilled a number of holes to permit the escape of the airstream. The desired humidity of each

air jet was obtained by mixing streams of dry and water-saturated air outside the choice chamber. The rate of airflow was controlled by screw taps and observed with mercury flowmeters. Experiments showed that an airflow of 600 ml./sec. on each side of the chamber, equivalent to an airspeed of 3·12 cm./sec. or 0·112 km./hr., was required to blow away the microclimate round the animals. This rate of flow was used in all experiments. The experiments were conducted in a constant temperature room at 20° C. In fluorescent light the animals were excited by the approach of an observer and the experiments were therefore performed in red neon light; in these conditions the animals did not appear to be disturbed by other movements in the room.

Before an experiment the crabs were placed in separate glass jars containing sufficient water almost to cover them and left in a constant temperature room. They were allowed a week to adapt to these conditions; during this period they were not fed. At the beginning of an experiment the animals were dried with a soft towel to remove any free water from the external surfaces and then placed singly and at random in the chambers. The desired humidities were found to be re-established a few minutes after replacing the lid. Position records were made as follows. A diameter was drawn across the false floor just above the centre partition: two lines 3 cm. from this diameter and parallel with it were also drawn. This 6 cm. wide central strip was designated the neutral zone. Crabs were recorded as being to right or left, or in this zone, if more than half the body was in a particular area.

Animals in the 20–30 g. weight range were used. No selection was made for sex.

Poynton (1954), working with frogs and using similar apparatus, found that as the speed of the airflow was increased the activity of the animals was depressed. Tests were made to see whether the selected speed of airflow affected the responses of *Potamon*. For this purpose the activity of crabs in still and moving air was compared. The chambers were used as uniform humidity chambers and experiments were conducted at 100% relative humidity (R.H.) to eliminate the possible effect on activity of the evaporating power of the air—for at humidities lower than 100% R.H. this would be greater in moving than in still air of the same humidity owing to the establishment, in the latter conditions, of a microclimate around the crab. Crabs placed in separate chambers, were observed at 3 min. intervals for 4 hr. and recorded as being 'active', 'inactive' or 'virtually inactive', the latter class covering any cases between the extremes of definite locomotor activity and complete inactivity. At intervals of 15 min. the animals were disturbed by a wire rod. Half of the crabs used were subjected to moving air during the first and third hours and the other half during the second and fourth hours. During the periods in still air the chambers were covered with unperforated lids. Twenty-eight specimens of *P. depressus* were used and yielded 1120 readings both in still and moving air. A summary of the results is shewn in Table VII. The activity in both cases is low: it will become apparent later that this low value is in keeping with the eccritic humidity of the crab. The differences between the two sets of values are not significant and it may be concluded that movement of air at a rate of 3·12 cm./sec. has no effect on activity.

TABLE VII

Effect of air-flow on the activity of *Potamon depressus*

	Number of animals			% of animals		
	Active	Virtually inactive	Inactive	Active	Virtually inactive	Inactive
Still air	108	553	459	9·6 ± 5·6	49·4 ± 9·4	41·0 ± 9·3
Moving air	143	428	549	12·8 ± 6·3	38·2 ± 9·2	49·0 ± 9·4

While moving air has no quantitative effect on activity, it does not necessarily follow that the crab will not show a preference when presented with a choice between moving and still air. This possibility was tested to ensure that the reaction of animals in humidity gradients would not be complicated by slight differences in air velocities on either side of the chamber, differences which arose from errors in reading the flow meters and were of the order of 0·2 cm./sec. A direct choice between moving and still air was considered impractical as an airflow through one half of the chamber might cause eddy currents in the half receiving no air current. The animals were therefore presented with a choice between two currents of saturated air, one moving at a rate of 3·12 cm./sec. and the other at 0·93 cm./sec. Crabs were placed singly in the chambers and their positions observed after one hour. Each animal was tested four times. External influences were controlled by presenting each animal twice with the fast current on one side of the chamber and twice on the other. A total of 168 position records were obtained using 42 specimens of *P. depressus*. On 26 occasions a crab was recorded as being in the neutral zone; of the remaining 142 readings, 71 shewed the crabs to be in the fast current and 71 to be in the slow. The crabs therefore do not show a preference between these air currents and it may be assumed that small differences in the airflow between the two halves of the chamber will not affect the humidity response.

RESULTS

The humidity response of *P. depressus* was first investigated. As a preliminary to this, the length of time required for the development of an equilibrium distribution was ascertained. The experiment was conducted in two humidity gradients, namely 100/50% R.H. and 100/75% R.H. Twenty-eight sets of observations were made in each gradient, external influences being controlled by presenting each animal twice with the upper humidity on one side, twice on the other side of the chamber. In both cases an equilibrium distribution was attained after approximately 50 min. In later experiments a period of one hour was allowed to elapse before observations on distribution were made. From our previous results it can be seen that very little desiccation will have taken place during that time.

The animals used came directly from water and when, just over an hour later, their positions had been recorded they were returned again to water and not used for at least another 4 hr. In this way any cumulative effect of desiccation was avoided. Each animal was tested four times in any one gradient and external influences were controlled as before. Twelve gradients were used and a total of 224

position readings from 56 animals taken in each gradient. The results obtained are shown in figure 7. The intensity of reaction is expressed as 100W/W + D where W is the number of animals in the humid side and D the number on the dry side of the chambers.

First, it will be seen that in all humidities there is a reaction towards the higher available humidity; the strong reaction in a gradient of 90/100% R.H. indicates that the preferred humidity lies within this range. Secondly, it is clear that the

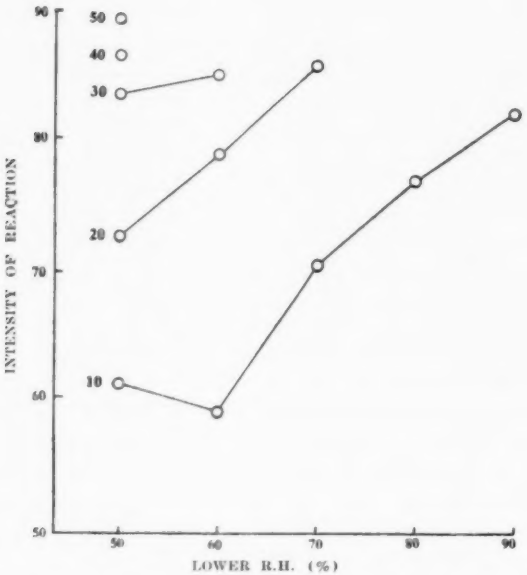

FIG. 7. Intensities of humidity responses of *P. depressus* in different gradients. The reaction intensity has been plotted against the lower available humidity, while points representing gradients of equal magnitude have been joined. The figures on the left hand of the curves show the magnitude of these gradients.

intensity of the reaction is influenced by the magnitude of the gradient presented and lastly that it is also affected by the particular value of the gradient, becoming more intense the more closely the upper available humidity approaches the eccritic value.

This double response both to humidity range and to the specific value of the gradient has been previously found in a number of arthropods shewing a preference for moist conditions. It is shewn by *Agriotes* (Lees, 1943), *Peripotopsis* (Bursell and Ewer, 1950), and *Porcellio* (Gunn, 1937), albeit the behaviour of this latter animal is more complicated than the others. The condition in *Potamon* is most closely

paralleled by that of the diplopod, *Orthomorpha gracilis* (Perttunen 1953), where the intensity of the reaction is correlated both with the higher available humidity and with the range of the gradient when the higher humidity falls below about 90% R.H.

Comparison of the Humidity Reactions of the Three Species

The reaction intensities of *P. sidneyi* and *P. warreni* in gradients of 90/80%, 90/50% and 70/50% were determined using the same technique. The results obtained are compared with those from *P. depressus* in Table VIII. In the gradient 90/80% the intensity of the reaction shown by *P. sidneyi* is significantly less ($P < 0.02 > 0.01$) than that of *P. depressus* or *P. warreni*; the difference between the latter two is not significant. In the gradient 90/50% the difference between *sidneyi* and *warreni* is significant at the same level, but the response of *depressus* is not significantly different from that of the other two species. In the gradient 70/50% R.H. there is no difference between the reactions.

Table VIII

Humidity responses of different species of *Potamon*

Gradient offered	Species	Observations Wet	Dry	Neutral	Reaction intensity (100W/W + D)
90–80	*sidneyi*	130	75	19	63·4
	warreni	151	58	15	72·2
	depressus	159	48	17	76·8
90–50	*sidneyi*	168	42	14	80·0
	warreni	199	17	8	92·1
	depresius	189	29	6	86·7
70–50	*sidneyi*	146	53	25	73·4
	warreni	155	50	19	75·6
	depressus	146	55	23	72·6

Unfortunately lack of material made it impossible to extend these observations, which do however indicate that the intensity of the humidity response of *P. sidneyi* is lower than that of the other two species when presented with a choice between 90% and a lower R.H.

III. THE 'WATER DRIVE'

The water drive was measured by the relative times spent in and out of the water over a fixed period. The crabs were kept singly in box compartments measuring 40 × 25 × 25 cm. A dish, 10 cm. in diameter and half filled with water, projected through a hole in the floor of the box. The edge of the dish was about 2 cm. above the floor and the crabs seemed to experience no difficulty in climbing in and out. A low guard rail round the dish prevented the animals from bumping accidentally into its side. The top of each compartment was covered with a sheet of glass, the experiments being conducted in regularly alternating light and dark.

Each dish rested upon one arm of a balanced see-saw device: when a crab entered the dish, the arm was depressed and, making a contact, operated a signal marker recording on a smoked drum.

Before an experiment the crabs were placed in glass jars and almost totally immersed in water. The jars were left in a constant temperature room at 20° C. for a week. The animals were fed at the usual time during this week, but were not fed during the subsequent experimental week. At the beginning of an experiment a crab was placed in each compartment and left to adapt to the general conditions in the compartment for 12 hr. before recording began. The water in the dishes was changed every two days. The crabs were subjected to 14½ hr. of artificial light each day, the periods of light and dark corresponding approximately to those outside the laboratory. These experiments were made during the summer months of September to February and, to control possible seasonal effects, experiments on the three species were run concurrently. Twenty animals of each species used were tested. Only females were used and as far as possible the animals were matched for size. From the traces the time spent in water was calculated and expressed as a percentage of the total time spent in the compartment.

The results for each species are shown in Table IX. *P. sidneyi* spent approximately twice as long in water as did the other two species. The difference is statistically significant ($P < 0.01$), while the slight difference between the means for *P. warreni* and *P. depressus* is not.

TABLE IX

'Water drive' of different species of *Potamon*

Species	Range of duration of experiments (hr.)	Mean duration	Mean time spent in water (%)	Mean maximal exposure time (hr.)
P. sidneyi	162·1–173·2	170·1	57·95 ± 2·24	11·3
P. warreni	162·1–193·4	170·1	30·98 ± 3·03	12·4
P. depressus	162·1–193·4	169·4	26·24 ± 2·76	13·6

The results were also analysed to see whether there was any difference in the time spent in water in the dark and in the light. The results are shown in Table X. The differences found are slight and insignificant for both *P. warreni* and *P. depressus*. On the other hand *P. sidneyi* spent a significantly greater time in water during the periods of illumination than it did during the dark periods. It will further be seen that, although *P. sidneyi* spends less time in water during the dark period than the light period, it nevertheless spends more time in water during the dark period than do the other two species.

TABLE X

'Water drive' of different species of *Potamon* in light and dark

Species	% of light time spent in water	% of dark time spent in water	P
P. sidneyi	65·00 ± 2·34	48·76 ± 2·55	< 0·01
P. warreni	28·34 ± 3·32	34·11 ± 2·95	> 0·1
P. depressus	27·69 ± 2·84	24·26 ± 3·19	> 0·4

It has previously been shown (Table III) that these crabs die after spending approximately 18 consecutive hours in moving air at 10% R.H., while they survive for about 160 hr. at 90% R.H. An analysis of the records was made to determine the maximal period each individual crab spent out of water. Of the 60 animals used, one specimen of *P. depressus* spent as long as 26·6 consecutive hours out of water; a further six, specimens of *P. depressus* and *P. warreni*, spent 20–25 hr. out of water while the remaining 53 animals were never out for as long as 20 consecutive hours. The R.H. within the compartments was found to vary between 65% and 75%. At 65% R.H. the expected survival time of *P. warreni* in moving air is 33 hr. and longer for the other two species. This is far longer than the maximal period of exposure found in these experiments where the air was still. It would appear therefore that the behaviour of the animals results in their returning to water long before they are in any danger of death by desiccation.

IV. RELOADING AFTER DESICCATION

An investigation of this aspect of the water economy was initiated after consideration of experiments on another amphibious animal, the toad. The evidence of R. F. Ewer (1952) and Jörgensen and Rosenkilde (1956) suggests that in *Bufo* secretion from the posterior lobe of the pituitary enhances the rate of water uptake after desiccation. Thus, in *Bufo regularis* Reuss, R. F. Ewer found that during the first 30 min. after desiccation, the rate of water uptake was six to seven times its normal value. She suggested that this effect might permit *Bufo* to absorb water rapidly from temporary supplies such as rain or dew and would explain its ability to exist for long periods without access to ponds. An analogous humoral control of water uptake in the crab might promote a rapid uptake on return to water, thus shortening the period in which desiccation would be damaging to the tissues.

Earlier investigations have suggested that hormones from the eyestalks of decapods can influence water uptake. Injection of decapod eyestalk extracts into frogs has been shown (Gray and Ford, 1940; Heller and Smith, 1948) to result in an increase in rate of water uptake. We have confirmed this result using extracts from *Potamon* injected into *Bufo regularis* and further find that there is no associated anti-diuretic effect.[1] Investigations of the effects of eyestalk ablation on crabs and crayfish have produced somewhat conflicting results. Thus Scudamore (1947) found that eyestalkless specimens of the freshwater crayfish *Cambarus immunis* Hagen maintained a higher water content than did intact animals. A similar effect has been shown in *Gecarcinus lateralis* (Frém) by Bliss (1953), but not in *Uca pugilator* (Bosc.) by Guyselman (1953). It is however to be noted that the effect reported by Bliss was only shown after a period of about 15 days and that Guyselman's experiments were not continued for so long a period. These various results all suggest that the eyestalk principle either inhibits water uptake or enhances urine outflow. There are

[1] It is possibly worth reporting that we have been unable to demonstrate any effect of mammalian pituitary extracts upon the water uptake of desiccated *Potamon*, whether normal or lacking their eyestalks.

also a number of experiments which demonstrate that the water uptake at moulting is greater in animals deprived of their eyestalks than in normal animals (Scudamore, 1947; Bliss, 1953; Carlisle, 1955). This is in keeping with the idea that the eyestalk produces a hormone which inhibits water uptake or acts upon the green gland so as to enhance urine output. On the other hand, Carlisle (1955) has found that removal of the eyestalks enhances the ability of *Carcinus moenas* (Penn) to withstand immersion in dilute sea water, a result which might be interpreted in the opposite sense.

Although no definite information is available for *Potamon*, in all decapods studied except the Anomura, the sinus gland-X organ complex is situated in the eyestalk and experiments were therefore undertaken to determine whether eyestalk ablation affects water uptake.

Material and Methods

All experiments were performed on *P. sidneyi*. The eyestalks were ablated at their flexible joints with fine scissors, excess loss of blood being prevented by sealing the wound with low melting-point wax. The operation was performed without the use of an anaesthetic. After the operation each animal was isolated for a period of at least a week before being used in an experiment. Isolation was desirable as the crabs become markedly more cannibalistic after eyestalk ablation, an effect also recorded by Scudamore (1947) in *Cambarus*. The mortality rate after the operation was high, usually in the region of 50% but sometimes as high as 80%.

At the beginning of an experiment the crabs were brought into water equilibrium by completely submerging them in running tap water for 24 hr. They were then dried by a standardized procedure to remove water from their external surfaces and weighed. This value is referred to as the 'equilibrium weight'. The crabs were placed over calcium chloride for about 24 hr. during which time they lost about 10% of the equilibrium weight. Finally they were returned to running tap water and weighed at regular intervals for a period of almost one hr.

The assumption was made that any increase in weight represented the amount of water resorbed. Short of blocking the anus and urinary papillae, and thus creating abnormal physiological conditions, no technique for controlling water loss in the faeces and urine was available. Experiments during which the animals defaecated were abandoned and it is doubtful whether the urine flow was copious enough to invalidate the assumption. Using tap waters coloured with different dyes, no evidence was found that desiccated crabs drink upon being returned to water.

There was no control of light or temperature, but the temperature of the tap water never varied by more than $\pm$ 0·5° C. during any one experiment. Animals were isolated from one another during the experiments and no animal was used more than once.

'Winter' Crabs

By accident rather than design the first series of experiments was performed during the winter months. The water temperature varied between 16° and 17° C.

Nine ablated and six normal animals, roughly matched for size, were used. For each interval the total increase in weight since desiccation, expressed as a percentage of the equilibrium weight, was calculated. The results are shown in figure 8a.

Although the increase in weight of both groups is approximately the same during the first interval, when water uptake may be taking place at a physical maximum, the rate of uptake of the ablated animals is higher than that of the normal ones in

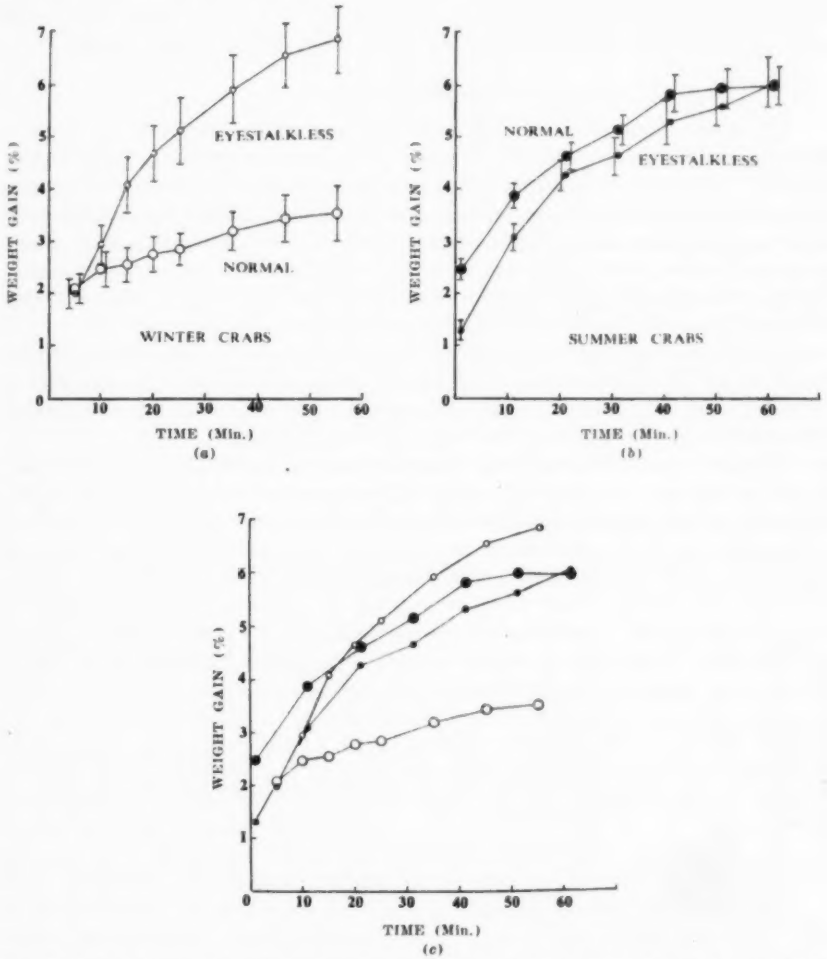

FIG. 8. Uptake of water, expressed as a percentage of equilibrium weight, with time of normal crabs (large circles) and eyestalkless crabs (small circles) in (*a*) winter (open circles), (*b*) summer (closed circles) and (*c*) summer and winter compared.

all the succeeding periods. In most cases a direct comparison of the means for operated and control animals during a single period shows the difference not to be significant. If, however, the readings for all intervals are taken into consideration and an analysis of variance performed using the values for the individual animals, then a value of $F\ 1/80 = 13{\cdot}21$ is obtained, corresponding to $P > {\cdot}001$. This indicates that taken over the whole experimental period the water uptake of the eyestalkless animals is significantly higher than that of the unoperated controls. These results imply that the presence of the eyestalk inhibits rather than enhances the rate of water uptake and are in keeping with the observations of Scudamore and Bliss.

'Summer' Crabs

The following summer, during some subsequent experiments designed for a different purpose, results were obtained which appeared to conflict with those just described and it was decided to repeat the experiment to see whether there was indeed a seasonal effect. The experimental technique was the same except that the initial weighing after desiccation was made after only one minute, and then subsequently at 10 min. intervals for an hour. The temperature of the tap water varied between 18° and 20° C. Nine ablated and nine normal animals were used; all were females. The results obtained are shown in figure 8b.

There is no apparent difference between the water uptake of the experimental crabs and of the controls. An analysis of variance on all the scores gave a value for F which indicated that over the whole experimental period the ablation did not have any significant effect on the rate of water uptake.

A direct comparison between the curves in figures 8a and 8b is shown in figure 8c. It will be seen that the differing 'winter' and 'summer' results are due, not to any difference in behaviour of the ablated crabs in the two seasons, but to a difference in the normal crabs. In summer these crabs showed a faster increase in weight than they had in winter and behaved as the ablated crabs did in winter. The implication is that in winter the eyestalk secretes a principle which curtails water uptake while in summer the secretion is smaller or ceases completely.

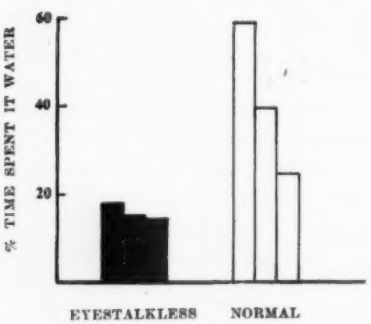

Fig. 9. Percentage time spent in water by winter crabs; on the right three normal animals, on the left three eyestalkless animals.

V. THE WATER DRIVE OF EYESTALKLESS ANIMALS

If eyestalk removal alters the rate of water uptake in winter, there may also be a correlated change in water drive. This possibility was tested in a limited number of experiments which, unfortunately, could not be further extended. The water drive was compared in normal eyestalkless animals during the winter.

The apparatus was the same as used in previous experiments on water drive. The experiments were conducted in total darkness in a constant temperature room at 20° C.

The results obtained from three ablated and three normal animals are shown in figure 9. Although the number of results is small they strongly suggest that the water drive of the eyestalkless animals is lower than that of the normal controls. This result may be correlated with the previous demonstration that eyestalk removal enhances the rate of water uptake in desiccated animals and might therefore be expected to reduce the time that they would have to spend in water to reload.

DISCUSSION

The experiments reported above are essentially of a preliminary nature. They show that the rate of water loss of *Potamon* is high compared with that of terrestrial insects, but low compared with that of terrestrial forms with moist skins, such as toads and earthworms or with abundant tracheal stigmata such as peripatus. *Potamon* is, however, better able to withstand desiccation than other fresh water decapod crustacea. Thus Bovjberg (1952) found that the crayfish *Orconectes propinquus* Girard and *Cambarus foediens* Cottle survive in still air at 66% R.H. and 20·5° C. for only 6 and 12 hr. respectively. At 60% R.H. and 20° C. *P. depressus* will survive for 30 hr. in moving air. It seems possible that this marked difference may be correlated with cuticular permeabilities and these in turn with osmo-regulatory mechanisms. Shaw (1959) has shown that *Potamon* produces an isotonic urine and has a highly impermeable cuticle compared with that of *Astacus* which like the American crayfish produces a hypotonic urine.

The success of the insects and arachnids is, in part, attributable to their possessing a layer of epicuticular wax. No such layer exists in *Potamon* although its potential value is illustrated by the results quoted in Table VI where it is shown that a layer of vaseline over the carapace, by cutting down the rate of water loss, more than doubles survival time in a strongly desiccating atmosphere. This lack of a layer of epicuticular wax is shared with other terrestrial or amphibious crustacea and Edney (1954) has suggested that in the isopods, which have invaded the land from the sea shore, a permeable cuticle has been retained as a temperature regulating mechanism. That cuticular permeability does permit some regulation of body temperature in *Potamon* may be seen from the results of preliminary experiments summarized in Table XI. The values shown are the maximal survival times of

TABLE XI

Maximal survival time (hr.) of different species of *Potamon* exposed to moving air at different temperatures and humidities

Temperature (° C.)	*P. depressus*		*P. warreni*		*P. sidneyi*	
	Dry	Humid	Dry	Humid	Dry	Humid
41	3	2	>3	1	6	1
35	>7	3	>13	5	>39	>39
31	26	>26	—	—	—	—

crabs in dry air (ca. 25% R.H.) and humid air (ca. 85% R.H.). Five crabs were used in each treatment. At 41° C. the greater longevity of the crabs in dry air is well marked, especially for *P. sidneyi*. At 35° C. the effect is obvious with *P. depressus* and *P. warreni*, while it is clear that *P. sidneyi* has a higher lethal temperature than either of these species. At 31° C. the effect, studied only with *P. depressus*, is reversed; this temperature lies below the lethal temperature for this species and the greater drying power of the dry air kills by desiccation. *Potamon*, however, has commenced its invasion of the land from the fresh waters and not across the shore and it may be that cuticular permeability has been retained as a respiratory adaptation rather than in relation to temperature control.

A comparative study of relative resistance to desiccation shows *P. sidneyi* to be the best adapted (Table XII), but in its behaviour it seems to be the most aquatic in habit and, at least when water loaded, it has the weakest response in a humidity gradient. These results appear contradictory. It must, however, be remembered that a weak response to humidity might permit *P. sidneyi* to invade areas which could not be entered by the other two species. Viewed in this light, its weaker humidity response possibly represents further adaptation to a terrestrial existence than is the case with *P. warreni* and *P. depressus*. The interpretation of the 'water drive' is less clear: certainly the tendency of *P. sidneyi* to leave the water more frequently by night than by day will offer it greater protection against desiccation, but it may be that the further differences between the species reflect some other facet of their biology, possibly different annual times of moulting or oviposition, and have no direct relation to their water economy.

TABLE XII

Comparison of the water economies of different species of *Potamon*

Parameter	*P. sidneyi*	*P. warreni*	*P. depressus*
Survival time (hr.) at 70% R.H.	62·1 ± 4·5	35·9 ± 2·3	46·0 ± 2·5
Intensity of reaction towards the wet in a gradient of of 80–90% R.H.	63·4	72·2	76·8
'Water drive' as % of time spent in water	58·0 ± 2·2	31·0 ± 3·0	26·2 ± 2·8

Table XII shows also that in terms of their water economy, *P. depressus* and *P. warreni* are very similar. Our field observations show that while either of these species may occur in the same locality as *P. sidneyi*, they are never found together. *P. warreni* has not previously been reported from Natal; it may be a recent invader from the Orange River System. It is possible that the similarity of water economy of *P. depressus* and *P. warreni* is an expression of a similarity of the ecological nitch of the two species and that their mutual exclusiveness reflects some type of competition for this habitat.

The experiments upon water reloading offer no evidence for the existence of a hormone which can specifically alter the rate of water uptake to meet the day-to-day variations in water requirements of a semi-terrestrial animal. They are most readily

interpretable in relation to the moulting cycle. Moulting in *Potamon* occurs during the summer, and it is to be expected that summer crabs will have a higher water permeability than winter crabs. Eyestalk ablation of winter crabs will, however, remove the source of moult inhibiting hormone and an increase in cuticular permeability will follow. Thus it comes about that eyestalkless winter crabs reload more rapidly than normal winter crabs and at about the same rate as normal and eyestalkless summer crabs.

The absence of any water-reloading adaptation correlates with the mechanism of osmo-regulation of *Potamon*. The urine is isotonic with the blood and salt loss is reduced to a minimum by the development of a very impermeable cuticle with a resulting low rate of urine formation (Shaw, 1959). The emphasis is upon impermeability and associated with this the animals do not drink. Clearly the mechanism of osmotic-regulation conflicts with any possibility of rapid reloading with water.

Despite its ability to withstand desiccation, *Potamon* is less successful as a terrestrial animal than many forms such as toads, slugs and peripatus less well able to retain water. It seems likely that the factor limiting *Potamon's* success is its inability to utilize minor sources of water such as dew fall and that in the first stages of evolution of a terrestrial fauna an ability to obtain water from such transient sources is more important than ability to retain water.

Acknowledgement

The Council of the Society desires to acknowledge a grant toward the cost of publication of this paper from the University of Natal.

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REGULARITIES INVOLVING $^{6}_{2}$He AND $^{8}_{2}$He AND THEIR POSSIBLE IMPLICATIONS FOR NUCLEAR STRUCTURE

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(Read August 17, 1960)

An examination of several types of evidence (systematics of stable isotopes, relative abundances of isotopes, energies of excited states, neutron and proton separation energies, mass excess and binding energy, and the half-lives of long-lived heavy alpha-active nuclei) reveals regularities associated with increases in the $^{6}_{2}$He sub-units as well as the more familiar $^{4}_{2}$He (alpha-particle) sub-unit. Several $^{8}_{2}$He regularities involve seven, but never more, participants. This corresponds to a total range of 36A and 12Z. A consideration of the regularities leads to the suggestion that if clusters occur on the nuclear surface—or perhaps within the structure—both $^{6}_{2}$He and $^{8}_{2}$He should be considered as possible clusters. On the basis of this assumption, a threefold division of nuclei with respect to Z and N is suggested:

(i) The $^{4}_{2}$He region. Up to Z = N = 20

(ii) The transition region. Between Z = N = 20 and N = 50

(iii) The $^{8}_{2}$He region. N = 50 to N = 152.

If it is assumed that heavy nuclei (N > 50) of a given type are 'built' by adding $^{6}_{2}$He clusters to the nuclear surface, the rate of increase of N-Z is a little too rapid for stability to be maintained over a large range of Z and an examination of the $^{8}_{2}$He regularities leads to the suggestion that one function of N = 82 and certain other significant neutron numbers may be to reduce neutron excess.

INTRODUCTION

The well known α-particle of the nucleus in which low A nuclei are considered to consist of aggregates of α-particles, has been given new impetus by the recent work of Wildermuth and Kanellopoulos (1958) on their suggested cluster model of the nucleus. These authors referred in particular to the nucleus $^{8}_{4}$Be, considered as two alpha-particle clusters, and pointed out that clusters other than $^{4}_{2}$He might be present in nuclei; they in fact pointed out that stable closed shells such as those of N = 50 and N = 82 could be regarded as large clusters. The idea of clusters in the nuclear surface has recently been discussed by Wilkinson (1959) and by McCarthy and Prowse (1960).*

The possibility of $^{6}_{2}$He ($2p + 4n$) as a cluster was mentioned by Ahrens (1957a) as a result of studies of the relative abundances of isotopes and arising from the idea of the cluster model, Ahrens and Cherry (1958) have commented further on this possibility.

Added in proof:

* Sheline and Wildermuth (*Nuclear Phys.* 21, 196, 1960) have recently discussed experimental evidence for cluster structures and refer to clusters of single nucleons, H^3, He^3, H^3, He^4 etc. and Selinov (*Proc. 2nd U.N. Int. Conf. Peaceful Uses At. Energy*, 30, 307) has referred to $2p + 2n$ (i.e. He^4) and $2p + 4n$ (i.e. He^6) in the formation of certain nuclei.

Their preliminary discussion, based on N,Z systematics of stable eZ—oN nuclei, was brief and it is the purpose here to present and discuss more fully certain evidence and regularities which appear important for nuclear structure considerations with respect in particular to the suggestion that $^{6}_{2}$He might be a cluster component of the nucleus. In addition to N,Z systematics on the relative abundances of isotopes, the other data which will be considered are: the energies of excited states of nuclei; neutron and proton separation energies; mass excess and binding energy; and, for nuclei with $Z > 83$, systematics of the half-lives of long lived α-active nuclei.

For the purpose of the present paper the term 'cluster' will be used to mean 'an aggregate of nucleons' which either at the nuclear surface, or possibly within its structure, may be regarded as having some stability. It is not assumed that such an aggregate must be completely stable when isolated (e.g. $^{4}_{2}$He) or that in the nucleus it exists as a permanent entity.

SOME REGULARITIES WHICH APPEAR SIGNIFICANT FOR STRUCTURE CONSIDERATIONS (WITH PARTICULAR REGARD TO THE EXISTENCE OF CLUSTERS)

1. Systematics of stable nuclei

If clusters exist in the nucleus or its surface one might expect the N,Z systematics of stable nuclei to show a tendency for stable nuclei to be separated from each other by such nuclear clusters (Ahrens and Cherry (1958)). Such tendencies are particularly apparent if stable *odd* A nuclei are considered. Even A nuclei are less satisfactory for this purpose, particularly for high A nuclei, because even Z elements usually contain several isotopes. After He ($Z = 2$) *all* elements up to Cl ($Z = 17$)—fourteen in all—contain one odd N isotope only and in each the neutron excess remains the same ($N - Z = 1$). For each species of odd A nucleus (eZ—oN or oZ—eN) the range in Z in these isodiapheric sequences is six which is the same as that obtaining in the long $^{6}_{2}$He sequences for odd A nuclei (see below). The range in A is $6 \times 4 = 24$. Up to $Z = 40$, $N = 50$, even Z elements contain only one odd N isotope (vanadium with two is an exception); above $Z = 40$, most contain two unless affected by the presence of magic numbers (below). Ahrens and Cherry (1958) referred particularly to odd A nuclei of the type, eZ — oN, and in an N — Z, Z diagram (their fig. 1) for these nuclei they noted that over the range $Z = 46$ to $Z = 60$, pairs of odd N isotopes are separated from neighbouring pairs by steps of 6A ($2p + 4n$) and that the regularities referred to as $^{6}_{2}$He sequences are broken by the well known magic number $N = 82$. Such $^{6}_{2}$He sequences and magic number discontinuities, together with other features, may be recognized in figure 1 of this

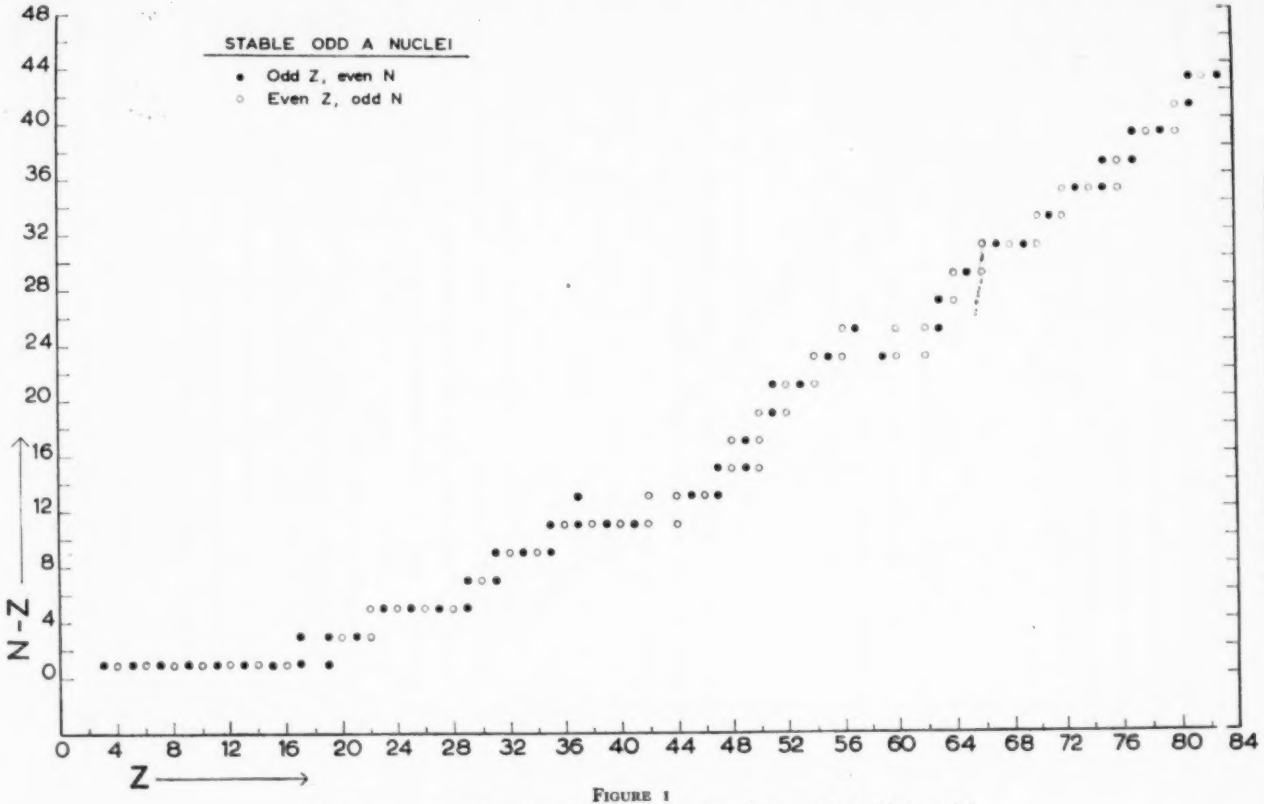

FIGURE 1
N–Z, Z diagram for all stable and long-lived (naturally occurring) odd A nuclei.

paper—an N − Z, Z diagram for *all* stable and long-lived (if radio-active, naturally occurring) odd A nuclei (eZ − oN and oZ − eN)—and more distinctly in figure 2 which refers to the region Z = 44 to Z = 83. Figure 2 shows that for oZ − eN nuclei, there is one complete long $^{6}_{2}$He sequence, from Z = 45 (Rh) to Z = 57 (La) and that for eZ − oN nuclei there are two long complete sequences, one from Z = 44 (Ru) to Z = 56 (Ba) and the other from Z = 60 (Nd) to Z = 72 (Hf).

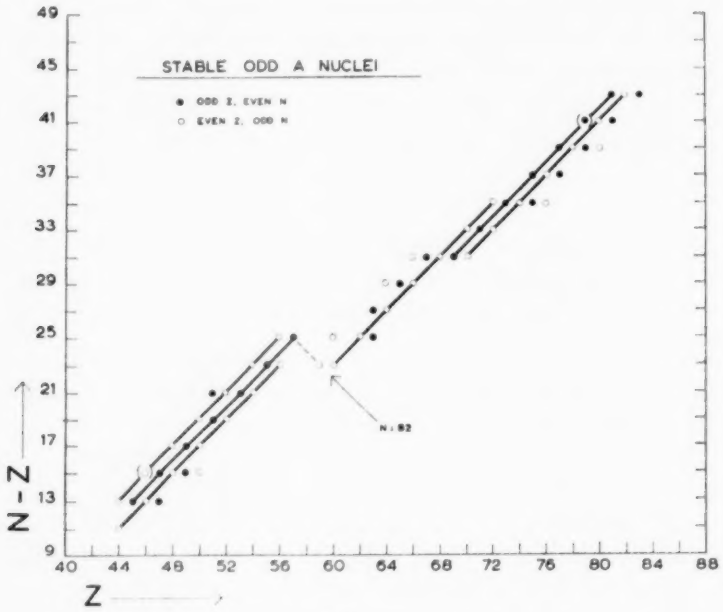

FIGURE 2

N–Z, Z diagram for stable odd A nuclei beyond Z = 44. The 'long' sequences are indicated by the joins. Note that each such 'long' sequence contains seven points and extends therefore over a range of 6Z and 36A (6 × $^{6}_{2}$He). Note also the effect of N = 82. Nuclei which are bracketed are radioactive (see text).

One incomplete (one component unstable) long sequence exists for each type of odd A nucleus: one from Z = 44 (Ru) to Z = 56 (Ba) and the other from Z = 69 (Tm) to Z = 81 (Tl).

Each of the longest sequences (complete or incomplete) contains 7 components and extends over a range of 6Z (36A). It may be noted that the 'missing' nuclide, $^{107}_{46}$Pd (N = 61) from the Z = 44 to Z = 56 sequence has an exceptionally long life, 7 × 10^{6} years; in fact this nucleus is the longest lived of all β-active eZ − oN

nuclei. (All β-active odd A nuclei which are longer lived and which are naturally-occurring, $^{87}_{37}$Rb, $^{115}_{49}$In, and $^{187}_{75}$Re for example, are of the type oZ − eN).

When stable oZ − eN nuclei alone are considered, the $^{6}_{2}$He regularities are not so clearly developed. Most odd Z elements contain one isotope only; 13 contain two in which case they are disposed about the so-called missing (no stable isotone) neutron numbers (Breusch, 1946; Ahrens, 1957a). Due perhaps to the effect of these missing neutron numbers, the $^{6}_{2}$He regularities are not so clearly developed in odd A nuclei of the type oZ − eN. Theoretical reasons have not yet been suggested to explain why the odd elements with two isotopes should be confined to the 'missing' neutron numbers. The reverse relationship appears to hold as well. Apart from the missing neutron numbers, each value of odd N contains one stable isotone, except N = 55 and N = 85 which contain 2; these are disposed about the two missing Z numbers, the radioactive elements Tc (Z = 43) and Pm (Z = 61). There are no exceptions.

2. Relative abundances (% proportions) of isotopes

The relative abundance (% proportions) of isotopes evidently depend both on the types of nuclear reactions which produced them and also on properties of nuclei, as, for example, structure. Although it is not possible to distinguish the effects due to these two factors and although relative abundance is not a property of the nucleus as such, it is clear that relative abundance is sensitively affected by certain well known shell numbers, N = 50 and particularly N = 82 for example. Thus, the most abundant isotopes (principal isotopes) of elements in the vicinity of these neutron numbers have either N = 50 or N = 82 (five elements have principal isotopes with N = 82) unless the nuclei lie close to the N,Z stability limits. Secondly, the elevation of relative abundance can be quite striking; for example, the relative abundances of the two magic number (N = 82) isotopes $^{140}_{58}$Ce (88·5%) and $^{138}_{56}$Ba (71·7%) are far greater (usually by × 2) than the relative abundances of all principal eZ-eN isotopes between N = 50 and N = 126. As therefore, relative abundance may be elevated by such highly favoured numbers as N = 50 and N = 82 particular attention will be given here to the most abundant isotopes of each element; in this respect, see also Ahrens (1957a).

The N,Z distribution of the principal isotopes (even Z and odd Z) is shown in figure 3. Six of the isotopes, $^{36}_{18}$A, $^{81}_{35}$Br, $^{108}_{46}$Pd, $^{109}_{47}$Ag, $^{194}_{78}$Pt, $^{112}_{74}$W, are not actually the most abundant isotopes of the respective elements but have been inserted in figure 3 for these reasons: As measured now, $^{40}_{18}$A is the principal isotope of argon, but as a major proportion of terrestrial $^{40}_{18}$A is evidently radiogenic (from K-capture decay in $^{40}_{19}$K; see Rankama (1954) for example) $^{36}_{18}$A, the next most abundant

isotope has been plotted. $^{81}_{35}$Br (48·5%) rather than $^{79}_{35}$Br (50·5%) has been plotted (but in parentheses) because of a better fit to the regularities in figure 3, and because the difference in relative abundance is very small it probably matters little, in any case, which isotope is chosen. Two other parenthesized points which appear in figure 3 belong to the isotonic pair $^{108}_{46}$Pd and $^{109}_{47}$Ag (N = 62). Neither is a principal isotope as $^{109}_{47}$Ag (48·65%) is a little less than $^{107}_{47}$Ag (51·35%) and $^{108}_{46}$Pd (26·8%) is slightly

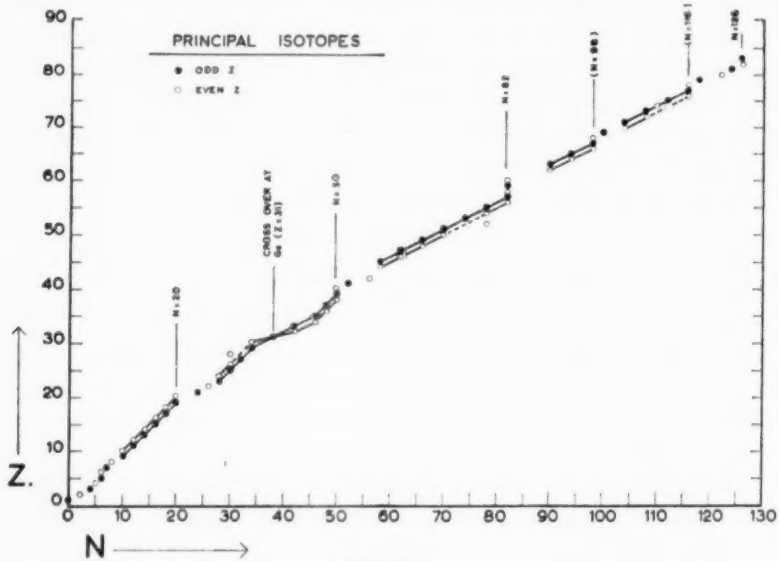

FIGURE 3

N,Z diagram for principal isotopes (eZ and oZ). Note (i) tendency for neighbouring principal isotopes to occur as isotonic pairs, (ii) effect of various neutron numbers, particularly N = 82 and (iii) cross-over at gallium (Z = 31). Neutron numbers which are not established magic numbers are bracketed (N = 98 and N = 116).

less than $^{106}_{46}$Pd (27·2%). As the differences are small, these isotopes are not seriously exceptional and as in Br above they have been plotted because of their precise fit in the sequences which follow N = 50 in figure 3. In platinum the most abundant even N isotope $^{194}_{78}$Pt (32·8%) is not actually the principal isotope because the *odd* N isotope $^{195}_{78}$Pt (33·8%) is slightly more abundant.

Several features are apparent in figure 3:

(i) a general tendency for the principal even Z and neighbouring odd Z isotopes to occur as isotonic pairs (Breusch, 1946; Ahrens, 1957a).

(ii) tendencies for such isotonic pairs to occur at intervals of 4A ($2p + 2n$) up to Z = N = 20 and of 6A ($2p + 4n$) for N > 50; between Z = N

= 20 and N = 50 steps of 4A and 6A exist. This 'transition' region (Ahrens, 1957a; Ahrens and Cherry, 1958) is discussed further below. The most fully developed pair of 6A sequences are from Z = 44 (Ru) to Z = 56 (Ba) and from Z = 45 (Rh) to Z = 57 (La) and are tabulated in Table 1. These correspond precisely in range with the longest sequences of stable odd A nuclei (eZ − oN and oZ − eN) discussed above. The occurrence of isotonic pairs in sequences is disturbed at the well known magic or shell numbers (N = 20, 50 and particularly 82) as well as at other numbers. Apart from a displacement at Z = 52 (Te; see Figs. 1 and 9 of Ahrens, 1957a) the $^{6}_{2}$He sequences are well developed and parallel. The effect of N = 82 is very marked indeed and five principal isotopes $^{138}_{56}$Ba, $^{139}_{57}$La, $^{140}_{58}$Ce, $^{141}_{59}$Pr and $^{142}_{60}$Nd) are isotonic at this highly significant neutron number. Isotonic $^{6}_{2}$He sequences begin again at N = 90 and are displaced at N = 98 and N = 116. These displacements at N = 98 and N = 116 together with a slight but nevertheless distinct elevation of the relative abundance (41%) of the principal isotope of osmium ($^{192}_{76}$Os) with N = 116 (see Ahrens, 1957a) may be taken to indicate that these two neutron numbers are also favoured.

(iii) cross-over at gallium (Z = 31). For light nuclei (< Z = 31), the odd Z component of the isotonic principal isotope has the greater neutron excess (by one), whereas for heavier nuclei (Z > 31) the reverse holds (Ahrens, 1957a). This relationship is disturbed by N = 50, N = 82 and other neutron numbers.

TABLE 1

Isotonic principal isotopes between N = 58($^{102}_{44}$Ru and $^{103}_{45}$Rh) and 'magic' N = 82($^{138}_{56}$Ba and $^{139}_{57}$La).

even Z	$^{102}_{44}$Ru	$^{108}_{46}$Pd	$^{114}_{48}$Cd	$^{120}_{50}$Sn		$^{130}_{52}$Te $^{132}_{54}$Xe	$^{136}_{56}$Ba
odd Z	$^{103}_{45}$Rh	$^{109}_{47}$Ag	$^{115}_{49}$In	$^{121}_{51}$Sb	$^{127}_{53}$I	$^{133}_{55}$Cs	$^{139}_{57}$La
N	58	62	66	70	74	78	82

For the purpose of further illustration and in order to show more clearly the variation of the important parameter, neutron excess, figure 4 relates N − Z to Z. This diagram clearly shows the presence of 4A sequences (slope zero) and 6A sequences (slope unity). Points have been joined according to the scheme adopted in figure 3.

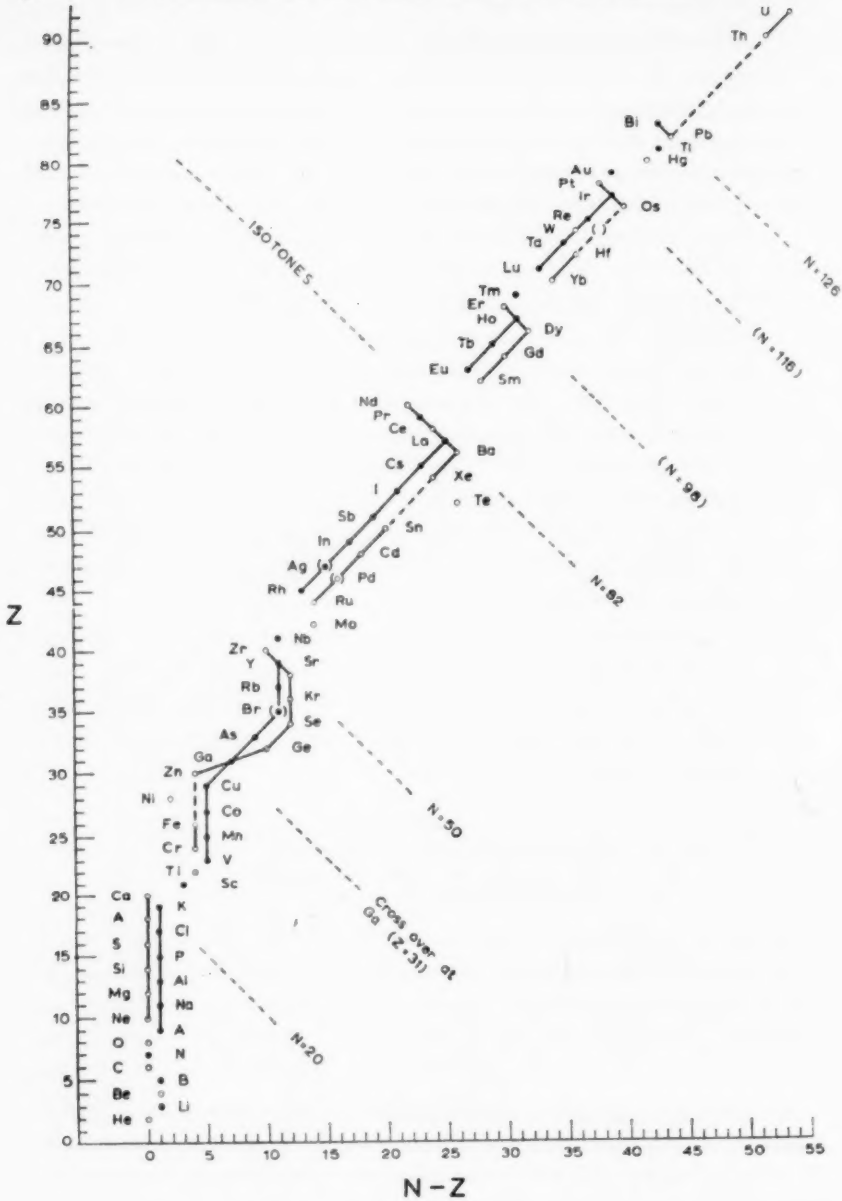

FIGURE 4
N–Z, Z diagram for principal isotopes.

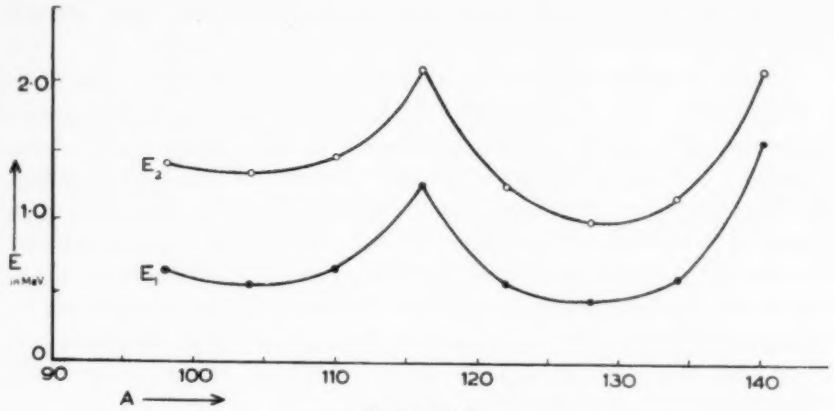

FIGURE 5 (*a*)

First and second excitation energies of e—e nuclei. The difference in A between successive nuclei is 6 ($2p + 4n$).

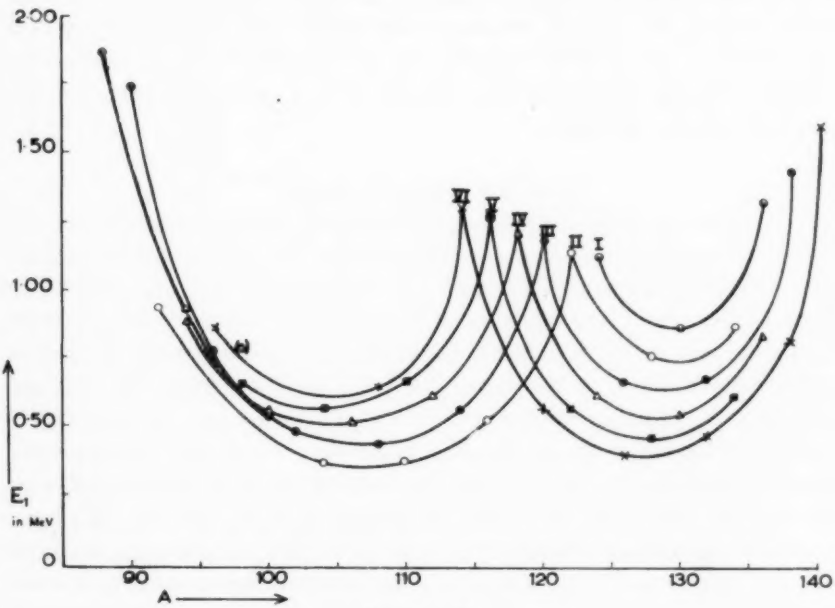

FIGURE 5 (*b*)

First excitation energies of $^{6}_{2}$He sequences of e—e nuclei. Note cross-overs of sequences.

3. SUNDRY OTHER DATA: ENERGIES OF FIRST AND SECOND EXCITED STATES; NEUTRON AND PROTON SEPARATION ENERGIES.

Cherry (in preparation) has investigated the properties of even – even nuclei over the specific range N = 50 to N = 82 for the purpose of uncovering possible regularities which might be taken to indicate the 'existence' of $^{6}_{2}$He clusters. As his discussion will be given in greater detail elsewhere a very brief outline is given here. The properties examined by Cherry are: energies of first and second excited states, neutron and proton separation energies, and the average binding energy per nucleon. The data are tabulated in the form of '$^{6}_{2}$He – sequences' and Cherry states that some of the regularities are striking and that 'if the idea of nucleon clusters in the nuclear surface is to be entertained seriously, it would appear that the possibility of $^{6}_{2}$He clusters existing in this region should be considered'. Two examples of such $^{6}_{2}$He regularities are given here (Figs. 5a and 5b).

4. MASS EXCESS (M – A)

Although the binding energy per nucleon B/A is a more fundamental nuclear property than M – A, mass excess is particularly sensitive for reflecting developments in the nucleus: shell closure at N = 50 and N = 82, for example. We will accordingly briefly examine this property with two objects in view: (i) as evidence in support of the existence of the so-called 'transition region' (see below) and (ii) to ascertain whether a smooth relationship exists between M – A and A for some of the $^{6}_{2}$He sequences already discussed.

(a) THE TRANSITION REGION

In a M – A, A diagram (Ahrens, 1957b), for all species of stable nuclei a well developed regularity extending over the range A ~ 60 to A ~ 90 was observed. It was noted further that the regularity was clearer, as expected, when only odd A nuclei were examined. The regularity becomes very well developed indeed, however, if only one type of odd A nucleus is considered. This is clearly shown in figure 6a which refers to the eZ – oN nuclei, $^{61}_{28}$Ni (N = 39), $^{67}_{30}$Zn, $^{73}_{32}$Ge, $^{77}_{34}$Se, $^{83}_{36}$Kr and $^{87}_{38}$Sr (N = 49) which are the only stable nuclei of this type over the range Z = 28 to Z = 38. This range corresponds precisely with the critical range of the 'transition' region (Ahrens, 1957b) which is suggested to extend from Z = N = 20 to N = 50. For Z < 28 > 38 the plotted points are distinctly displaced (Fig. 6b). This figure shows the disposition of the oZ – eN nuclei about the eZ – oN regularity. If the odd Z elements contain one isotope only (As and Y) fit appears perfect, otherwise if two isotopes are present (Cu, Ga, Br and Rb) the plotted points are very slightly displaced, as indicated.

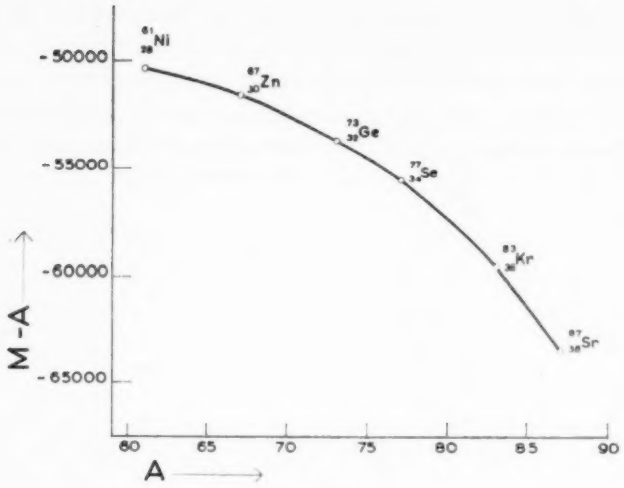

FIGURE 6 (*a*)

The relationship between M−A and A for stable eZ−oN nuclei over the 'critical' region (Z = 28 to N = 50) of the 'transition' range (Z = 20 to N = 50).

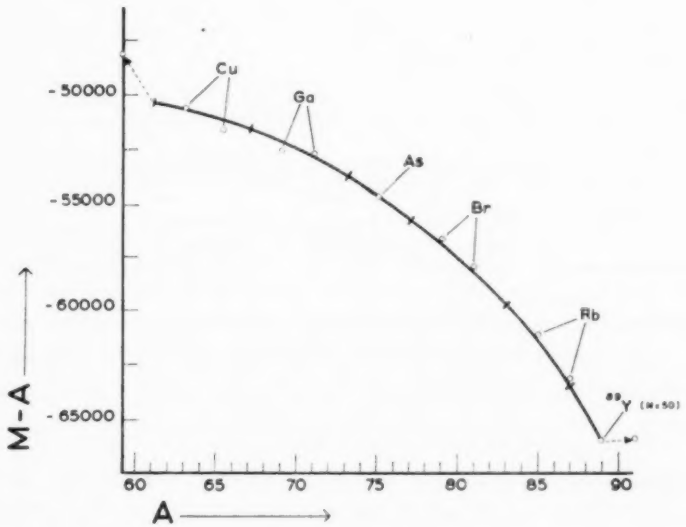

FIGURE 6 (*b*)

Disposition of stable oZ−eN nuclei about eZ−oN regularity.

The regularity in figure 6a may be expressed mathematically by the following equation obtained by the method of least squares:

$$9A^3 - 1001{\cdot}7A + 1{\cdot}6 \times 10^{-5}(M - A)^2 + (M - A)\,2{\cdot}49 + 1{\cdot}125 \times 10^5 = 0$$

A test by the χ^2 method shows the equation to have a very close fit. The full significance of this relationship is not clear, but we may conclude thus: the M − A, A

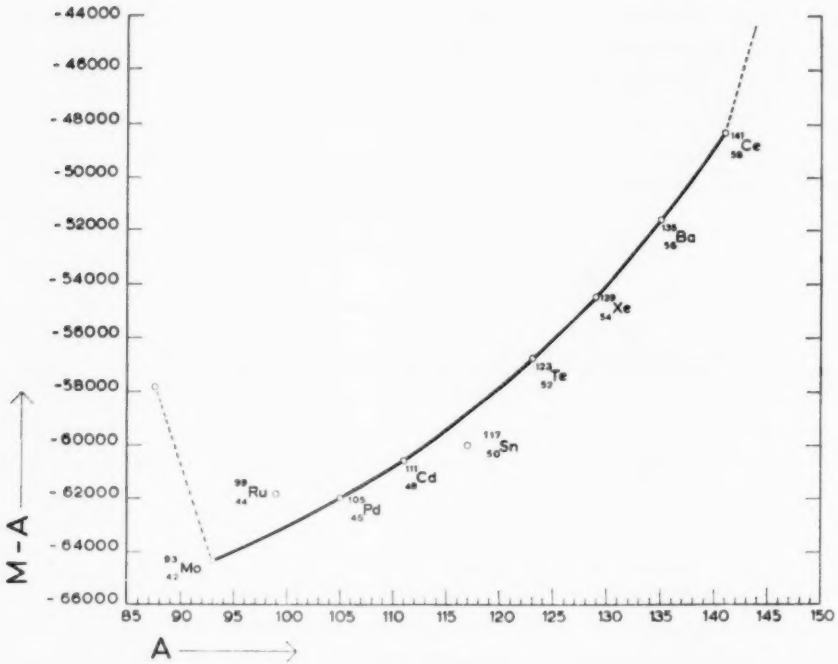

FIGURE 7

The relationship between M−A and A for stable eZ−oN nuclei over the range $^{93}_{42}$Mo to $^{141}_{58}$Ce.

regularity is quite remarkably well-developed and as its limits closely match the 'critical' region indicated by relative abundance data, this may be taken as further evidence in support of such a region.

(b) M − A, A REGULARITY FOR THE $^{6}_{2}$He SEQUENCE, Z = 46 TO Z = 58

Between N = 50 and N = 82 smooth relationships between M − A and A have been found for a number of $^{6}_{2}$He 'sequences'. One such regularity is shown here for illustration: namely, that involving the eZ − oN nuclei $^{93}_{42}$Mo, ($^{99}_{44}$Ru), $^{105}_{46}$Pd, $^{111}_{48}$Cd, ($^{117}_{50}$Sn), $^{123}_{52}$Te, $^{129}_{54}$Xe, $^{135}_{56}$Ba and $^{141}_{58}$Ce (fig. 7). The nucleus $^{99}_{44}$Ru is

distinctly displaced from the apparent regularity as is also $^{117}_{50}$Sn with 'magic' Z = 50. Nuclei with N = 50 and 82 are also sharply displaced, as indicated.

The regularity in figure 7 may be expressed mathematically by the following equation obtained by the method of least squares:

$$4A^2 + 141.\,OA + 2{\cdot}5 \times 10^{-6}(M - A)^2 - 0{\cdot}43(M - A) - 1{\cdot}81 \times 10^5 = 0$$

On testing by the χ^2 method this equation showed an extremely good fit.

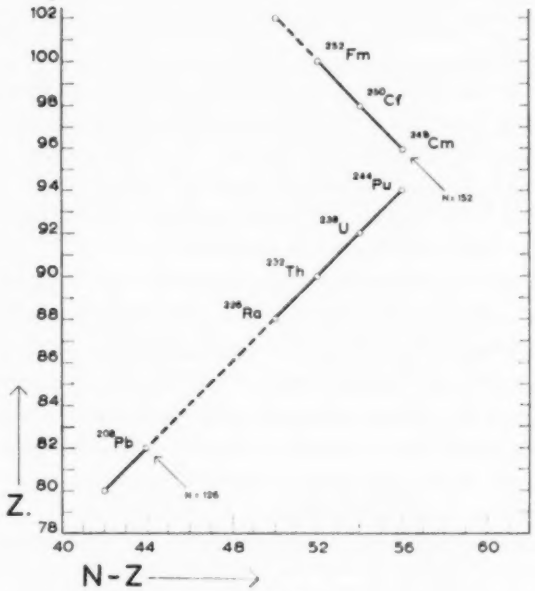

FIGURE 8

N−Z, Z diagram for longest-lived α-active e−e nuclei of the elements Ra, Th, U, Pu, Cm, Cf, Fm and X.

The existence of well-developed smooth regularities for given types of nuclei (e − o, o − e) involving increments of 6A may be taken as evidence in support of the possibility of the stability of $^{6}_{3}$He clusters in heavy nuclei.

The expressions above may be compared with Eqs. 3b and 5 of Levy (1957), which for stable nuclei of a given type (e − e, e − o etc.) becomes one in which △M is parabolic in A.

5. HALF-LIFE REGULARITIES OF α-ACTIVE NUCLEI

It is generally assumed that the rate of decay of a nucleus may serve as a very approximate index of nuclear stability. In which case the thorium isotope, $^{232}_{90}$Th

with its extremely long half-life ($1{\cdot}3 \times 10^{10}$ years) may be considered as a particularly favoured nucleus in the heavy A region, $Z > 83$. The next longest-lived isotope $^{238}_{92}U$ is 6A ($2p + 4n$) lighter than Th^{232}. Passing to lower Z, the longest lived isotope at $Z = 88$ (Ra) is Ra^{226}, 6A lower than Th^{232}, and continuing to higher ($Z > 92$) the longest lived isotope Pu is $^{244}_{94}Pu$. These four longest lived e – e nuclei of succeeding even elements form therefore an $^{6}_{2}He$ sequence. If extended to lower Z, the sequence does not include the longest lived isotopes of Rn and Po, but does include $^{208}_{82}Pb$ ($N = 126$); the range in Z and A from $^{208}_{82}Pb$ to $^{244}_{94}Pu$ is 12 and 36 respectively.

The $^{6}_{2}He$ sequence does not extend beyond $^{244}_{94}Pu$. The longest-lived e – e isotope of Cm is $^{248}_{96}Cm$, with $N = 152$. Thereafter the longest-lived even A isotopes for each succeeding even element are isotonic ($N = 152$). It has been suggested (Ghiorso, Thompson, Higgins, Harvey and Seaborg, 1954) that this neutron number represents a sub-shell—or, at least, a favoured number—and the half-life systematics evidently may be taken to support this suggestion.

The features noted above are clear in figure 8 an N – Z, Z diagram showing the longest-lived e – e nuclei in the region $Z > 82$. In this respect we may recall the observations by Perlman, Ghiorso and Seaborg (1950) and by Studier and Huizenga (1954). Perlman *et al* state, 'It will be recalled that in the region from lead to uranium there are added on the average almost *two neutrons for each proton* in attaining a comparable configuration with respect to α-stability for succeeding elements' (Italics inserted). Two neutrons for each proton is equivalent to an 6A ($2p + 4n$) increment when passing from one nucleus type (e.g. e – e) to the next.

Studier and Huizenga (1954) examined alpha and spontaneous fission half-lives and found that when the ratio $\frac{\text{alpha half-life}}{\text{spontaneous fission half-life}}$ was related to $\frac{Z^2}{A}$ much better-developed regularities were obtained if 6A intervals rather than 4A were used.

DISCUSSION

1. $^{6}_{2}He$ (AND $^{4}_{2}He$) AS POSSIBLE NUCLEAR CLUSTERS AND A TENTATIVE 3 FOLD DIVISION OF NUCLEI

The above three observations and comments ((i) long lived α-active nuclei; (ii) statement by Perlman *et al*; (iii) observations by Studier and Huizenga) together with the large number of regularities discussed before lead to the conclusion that if clusters do exist either in the nucleus or its surface, serious consideration should be given to $^{6}_{2}He$ as a possible cluster. The isolated nucleus $^{6}_{2}He$ is itself unstable (half-

life = 0·8 seconds) but such instability does not necessarily imply total instability on the surface or within a heavy nucleus: in this respect we recall the instability of the isolated neutron (half-life 13 minutes) which for many purposes is treated as a stable nuclear entity. For the sake of further discussion, let us assume that $^{6}_{2}$He, together with the alpha particle ($^{4}_{2}$He), are nuclear clusters. If so, the following 3-fold division and description of nuclei based on the regularities of this paper and a brief outline by Ahrens and Cherry (1958) is tentatively suggested:

(i) THE $^{4}_{2}$He (OR α-PARTICLE) REGION

Up to N = Z = 20, $^{4}_{2}$He is regarded as the principal nuclear cluster. Shell closure (possibly of clusters) takes place at Z = N = 20.

(ii) THE TRANSITION REGION

Z = N = 20 to N = 50. $^{4}_{2}$He and $^{6}_{2}$He as clusters outside a closed shell. The transition region is itself divided into two regions, one of which Z = 28 (or A = 60) to Z = 40, N = 50 (A = 90) is referred to as the 'critical' region.

(iii) THE $^{6}_{2}$He REGION

N = 50 to N = 152. $^{6}_{2}$He is regarded as the principal cluster after shell closure at N = 50. The region is best developed between N = 50 and N = 82 insofar that most $^{6}_{2}$He regularities are most highly developed between these two neutron numbers. The $^{6}_{2}$He cluster is perhaps arranged in sub-shell clusters containing a maximum of six such clusters per sub-shell.

2. A POSSIBLE ROLE OF THE IMPORTANT 'SHELL' NUMBER N = 82

The proposition that an excess of neutrons is required in comparatively heavy nuclei to overcome the effects of Coulombic repulsion is generally accepted. Neutron excess is zero in an alpha-particle and remains zero in the isodiapheric sequence of principal isotopes, $^{4}_{2}$He, ($^{8}_{4}$Be; unstable), $^{12}_{6}$C, $^{16}_{8}$O, $^{20}_{10}$Ne, $^{24}_{12}$Mg, $^{28}_{14}$Si, $^{32}_{16}$S, $^{36}_{18}$A and $^{40}_{20}$Ca. Consider heavier nuclei and particularly the region N > 50. Here N − Z increases more or less steadily for stable nuclei. For the whole range of Z, the smoothed relationship is sometimes expressed mathematically (Evans, 1956) thus:

$$N - Z = \text{const } A^{5/3}$$

or, in a more complicated form, as derived from the liquid drop model (Evans 1956). If it is assumed that in the region N > 50 successive heavier nuclei of a given type are built up of $^{6}_{2}$He entities, the rate of increase of N − Z with respect to Z is unity; this is greater than that given by the above expression and is evidently too rapid for stability (see also Ahrens and Cherry, 1958). In that case, N = 82 and certain other neutron numbers may perform the function of reducing neutron excess. This seems to be achieved in two ways. Consider the principal isotope diagram (fig. 4). At

$N = 82$ itself, neutron excess decreases because several principal isotopes are isotonic; secondly, the principal isotope sequences on either side of $N = 82$ are displaced in such a way that sequences beyond $N > 82$ are displaced towards lower $N - Z$ relative to those with $N < 82$. (Similar displacements, but on a smaller scale, are evident at $N = 108$ and $N = 116$.) Similar displacements are clear for the odd A nuclei (fig. 2) if the long sequences are examined.

ACKNOWLEDGEMENTS

Grateful acknowledgements are made to Mr. R. D. Cherry of the Physics Department for helpful discussions and useful suggestions and to Dr. E. Sohn of the Department of Mathematics for her aid in deriving the two mass expressions given in this paper.

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